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An updated checklist of the amphibian diversity of Maliau Basin Conservation Area, Sabah, Malaysia

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Abstract

The current account presents the results of a 14-day amphibian survey at Maliau Basin Conservation Area (MBCA). With a total of approximately 170 man-hrs, 44 species were detected at four study sites during the field period; four more species were later discovered outside the two-week campaign. The results are compared to the results of previous surveys. Apart from adults, we present the first photographic documentation of the larval stages of *Chiromantis inexpectatus* and Bornean *Phrynoidis juxtaspera*, along with a brief tadpole description; the better-known tadpoles of four more species were recorded. The results of our expedition suggest that nine more species are present at MBCA than reported by previous studies. We present an updated list of known species in the MBCA, comprising 61 species. The species accumulation curve over the 14 days period of the core survey did not show signs of asymptotic saturation. We conclude that the definitive species number for MBCA amphibians has the potential to increase with more thorough surveys in the future.

Introduction

To the general public, the amphibian species of East Malaysia (Sabah and Sarawak, Borneo) may seem to be relatively well-known. Particularly, the books by Inger (1966), Inger and Tan (1996), Malkmus et al. (2002), Imbun (2014), and Inger et al. (2017) give excellent summaries on the frogs of East Malaysia. Additionally, a widely-used internet resource provides an illustrated introduction to Bornean frogs and tadpoles (Haas et al. 2018). In the late 20th and early 21th centuries, several workers have contributed to our knowledge of the frogs of Sabah (for example, Inger 1966, Matsui 1979, Inger and Tan 1996, Malkmus et al. 2002, Kueh 2004, Kueh et al. 2004, Kueh and Maryati 2005, 2008, Shimada et al. 2007, 2008, 2011a,b, Matsui et al. 2007a,b, 2013a,b, Imbun 2014, Dehling et al. 2016). In recent years, research on East Malaysian amphibians, however, has not only redefined species and discovered new species (Waser et al. 2016, Dehling and Dehling 2017), or described their larval forms (Oberhummer et al. 2014, Shimada et al. 2015), but furthermore, revealed a substantial underestimation of alpha-diversity by uncovering cryptic species (e.g., McLeod 2010, Matsui et al. 2016). The emerging pattern of high diversity on a relatively small geographic scale includes high levels of micro-endemism, i.e., species with small distributional range, these are often montane species (Dehling 2008, Hertwig et al.

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2014, Waser et al. 2016). Furthermore, knowledge about the basic ecology of Bornean frogs is still in its infancy but has progressed recently (e.g., Inger 2009, Keller et al. 2009, Konopik et al. 2015, Pui and Das 2016, Goutte et al. 2017, Goyes Vallejos et al. 2017). The aforementioned recent systematic work and the emergence of high levels of genetic diversity let us predict that earlier accounts will quickly be outdated and will be in need of revision, and secondly, far more strategic sampling efforts will be needed to fully understand the alpha- and beta-diversity, distribution patterns, and evolutionary history of Bornean amphibians. It cannot be stressed enough that collecting specimens and tissue samples, and depositing them with proper scientific data in accessible museum collections is indispensable in order to answer questions of biodiversity, biogeography, ecology, and evolution.

The State of Sabah has created a number of national parks and conservation areas of various protection levels. Maliau Basin Conservation Area (MBCA) stands out among them because it had not been explored until quite recently. Difficulty in access to the area and rugged terrain have long been major obstacles for scientific exploration. The first major scientific expedition was conducted in 1988 by Yayasan Sabah Group and WWF-Malaysia. A major scientific expedition followed in 1996 (Maryati et al. 1998). MBCA comprises the Maliau Basin (58,840 ha; mostly primary forest, protected since 1981, plus surrounding forested buffer areas, comprising some 132,794 ha; Greer 2002, Yayasan Sabah 2014).

The Maliau Basin is an almost circular, saucer-like geological structure, approximately 25 km in diameter, and comprising Neogene mudstone and sandstone deposits (Hazebroek et al. 2004, Tongkul and Chang 2012). The alternating sandy and muddy deposits stem from a coastal environment and were sedimented during the Early Miocene and subsequently deformed during the Mid and Late Miocene, leading to layers dipped to various degrees (Tongkul and Chang 2003, Tongkul 2015). The sandstone-mudstone structure of the basin and erosion through geological time lead to the formation of 28 documented waterfalls with more than 5 m in height (Tongkul 2015). Maliau Basin is one in a series of similar saucer-shaped basins in northern Borneo. A steep escarpment to the outside of the rim separates and isolates it from neighboring forests. Its geological structures range from approximately 300 m to 1,675 m a.s.l. Vegetation zones stretch from lowland mixed dipterocarp forest to upper montane mossy forest at the rim (Webb and Ali 2002, Hazebroek et al. 2004). The only access to the basin is in the southeastern part with Maliau Gorge, where Sungai Maliau exits the basin. Inside MBCA, only a minor part can be reached by trails.

Considering the relative short period of scientific exploration, it is not surprising that there is still no comprehensive amphibian inventory of the Maliau Basin. A first list of amphibian species was published in Ahmad and Wong (1998). Traeholt (2001) issued a technical report summarizing the preliminary results of several survey excursions to nine sites at MBCA. Hazebroek et al. (2004) compiled a list from Ahmad and Wong (1998) and Traeholt (2001). Kueh and Maryati (2005) listed 24 species of frogs for MBCA, however, mostly relying on the list by Ahmad and Wong (1998), while adding some records for the Agathis Camp area. Chung (2006) gave a brief account of Maliau Basin, while Traeholt et al. (2007) published their earlier report in greater detail. Apart from their own findings, Traeholt et al. (2007) assimilated in their species list, the findings of Ahmad and Wong (1998) and Lakim and Yambun (2002), making their list the hitherto most complete account of the known amphibian species at MBCA. It comprised 54 taxa, of which 47 were named species and seven were unidentified taxa that could only be assigned to the genus level (marked "sp." in their list). Since then, two additional species have been described from MBCA, i.e., *Rhacophorus borneensis* (Matsui et al. 2013b) and *Chiromantis inexpectatus* (Matsui et al. 2014).

In early 2017, we were granted the opportunity to conduct a rapid amphibian survey of Maliau Basin. Time and manpower were limited, so that a complete list of all MBCA amphibians could not be expected. Yet, in the light of the poor knowledge of the Maliau Basin fauna, we present our report with the following objectives: 1) to present the account of species found during our survey; 2) to discuss earlier accounts and make these, sometimes difficult to find sources, better known to the international community; 3) to include photographic documentation for easy species identification; 4) to update the list of known and documented species of MBCA, applying current nomenclature. We hope this report stimulates further research on the amphibians of the Maliau Basin towards a comprehensive amphibian inventory and a better understanding of amphibian communities at MBCA.

Materials and methods

Field work was mainly conducted from 16 February 2017 to 2 March 2017. With respect to a comprehensive species list, additional photographic evidence by one of us (MBA) was added but was not restricted to the survey period and localities. In the following, we refer to these four main collecting sites (camps), including areas that could be reached from those sites during transect walks:

1) Study Center (4.734635°N, 116,975444°E; 260 m a.s.l.) and surroundings, including Belian Trail and Sungai Maliau and its tributaries within 2 hrs walking distance from Study Center; sampling effort: 60 man-hrs.
2) Agathis Camp (4.697934°N, 116.9069°E; 531 m a.s.l.); sampling along the river; sampling effort: 20 man-hrs.
3) Ginseng Camp (4.744990°N, 116.918209°E; approx. 660 m a.s.l.); sampling the stream above and below Ginseng Falls; sampling effort: 30 man-hrs.

4) Nepenthes Camp (4.733450°N, 116.877945°E; approx. 1,050 m a.s.l.); sampling was done along the existing trails within a radius of approx. 4 km around the camp; sampling effort: 60 man-hrs.

Surveys at each of the sites where conducted mostly between 19:00–24:00 h. Specimens were collected during nightly transect walks and included visual and acoustic encounter techniques (Rödel and Ernst 2004). The respective habitats where searched for both adult and larval stages.

Living specimens were photographed with a Canon 5D IV camera and Cannon 100 mm macro lens (for adult frogs) or a Fujifilm X-T2 camera and Fujinon 60 mm macro lens (tadpoles), some under field but mostly under laboratory conditions with double flash lighting. Photos were taken in RAW format and subsequently developed in Capture One 10 or AfterShot Pro3 software. Voucher specimens were euthanized with an aqueous chlorobutanol solution (adults) or Eugenol (Guenette et al. 2007) added to water (tadpoles). Voucher specimens (Appendix 1) and tissue samples were taken in the field and deposited and registered at the BORNEENSIS herpetological collection at Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Kota Kinabalu or at the Natural History Museum Bern (NMBE). Tissues were preserved in RNALater®; tadpoles and frogs were fixed in 4% neutral-buffered formalin. After fixation, frogs were rinsed and transferred to 70% ethanol, whereas tadpoles were stored in buffered 4% formalin. Tadpoles were deposited and catalogued at the Zoological Museum Hamburg (ZMH).

Taxonomy follows Frost (2018). Species determination was primarily accomplished using morphological criteria (Das et al. 2007, Inger 1966, Inger et al. 2017, Malkmus et al. 2002). However, in some groups under taxonomic investigation (see in Results and Appendix 1: Specimen vouchers sections for details), DNA barcoding was applied and comparisons to available GenBank sequences were made to assign the larval stages unequivocally to the sympatric adults (*Chiromantis*, *Phrynoidis*) and to identify the species of certain genera, notably *Ansonia*, *Kalophrynus*, *Limnonectes*, *Philautus* and *Meristogenys*. Genomic DNA was extracted from liver, thigh muscle tissues or, in case of tadpoles, from tail muscle using Wizard SV Genomic DNA Purification System (Promega, Switzerland) following manufacturer's protocol.

The following primers were used: For the *Chiromantis* and *Phrynoidis* tadpoles we used 12sm: 5'-GGCAAGTCGTAACATGGTAAG-3' and 16SD: 5'-CTCCGGTCTGAACTCAGATCACGTAG-3' (Pauly et al. 2004), annealing temperatures 51°C; it yielded partial tRNA-Val and 16S rRNA gene sequences. For adults we applied 16SC Sequence 5'-GTRGGCCTAAAAGCAGCCAC-3' and 16SD primers. PCR reactions were prepared with a 25-µl PCR reaction volume containing 2 µl of DNA, 12.5 µl of GoTaq Hot Start Green Master Mix (Promega), 1 µl of each primer (10 µM), and 8.5 µl ddH2O was used. The cycling conditions for 16S rRNA were as follows: denaturation at 94 °C for 2 min, 5 cycles at 94 °C for 30s, 48.2 °C for 30 s, and 72 °C for 1 min, followed by one final extension at 72 °C for 5 min. PCR products were cleaned using Wizard SV Gel and PCR Clean-Up System (Promega). PCR products were excised from agarose gels and were either purified with ExoSAP-IT or with Wizard SV Gel (Promega). Sanger sequencing was done by LGC Genomics (Berlin, Germany) or Macrogen (Korea). Sequences were checked for ambiguities, assembled, aligned, and analyzed in Geneious Pro 7.0.6 and 9.1.8 (http://www.geneious.com, Kearse et al. 2012).

Results

Between 16 February–2 March 2017, a total of approximately 170 man-hrs was expended and 44 species of frogs were detected at four study sites within MBCA (Table 1); four more species were documented photographically outside this study period. Altitudinal range of sampling was approximately 260–1050 m a.s.l. Previous studies were evaluated (Ahmad and Wong 1998, Lakim and Yambun 2002, Norhayati et al. 2010, Traeholt et al. 2007) to compile an updated species list for MBCA (Table 2). The following species below were encountered during the two-week survey. Short descriptions and comments are given for each of the species. For voucher specimens, collection numbers (HEP, NMBE, ZMH) are provided for future reference in the Appendix 1: Specimen vouchers section below. The species found at each of the study sites during our survey are given in Table 1.

Bufonidae, True Toads

Ansonia sp; Fig. 1a

Snout obliquely protruding in lateral view; snout tip pointed in lateral view; body generally slender; dorsum brown to olive, with blurred dark markings; finely warted dorsally, warts without keratinized spines; dorsolateral warts slightly larger, some fused to form a ridge from above tympanum to shoulder; belly gray with dense brown spots; throat dark brown; light marking under the eye and between angle of jaw and shoulder; toes and fingers possess rounded, slightly swollen tips; iris black with dense golden iridophores; more reddish in anterior and posterior sector; tympanum distinct, small.—This species was common at Fawzy Fall near Nepenthes Camp. Specimens were observed at or in the stream, sitting on low vegetation or rocks.

Genetic barcoding and sequence analysis (see Appendix 1: Specimen vouchers section for accession numbers) suggest that this population is conspecific to the unnamed clade *Ansonia* sp. 3 in Matsui et al (2010) from the Kelabit Highlands in northern Sarawak.

Table 1. List of anuran species encountered at MBCA with the species composition present at four different sites. + = specimens recorded during a two-week survey at Maliau Basin Conservation Area (MBCA), voucher specimens were collected; **c** = present during two-week survey, identified by call, not collected; **p** = additional species photographically recorded outside the two-week study period, not collected. With reference to Matsui et al. (2016), we list four genetically divergent lineages of Creek Frogs ("*kuhlii*"-complex).

Taxon	Agathis Camp	Ginseng Camp	Nepenthes Camp/Trails	Study Center/Trails/Maliau
	531 m a.s.l.	660 m a.s.l.	1060 m a.s.l.	260 m a.s.l.
Bufonidae				
Ansonia sp.			+	
Ansonia leptopus				+
Ansonia longidigita		+		
Ansonia spinulifer		+		
Ingerophrynus divergens	+			+
Leptophryne borbonica		+		
Phrynoidis juxtasper	+		+	+
Dicroglossidae				
Fejervarya limnocharis				+
Limnonectes ingeri				+
Limnonectes sp. ("*kuhlii*" Lineage 2)	+			+
Limnonectes sp. ("*kuhlii*" Lineage 5)		+	+	
Limnonectes sp. ("*kuhlii*" Lineage 12)				+
Limnonectes sp. ("*kuhlii*" Lineage 17)		+		
Limnonectes leporinus	+	+		+
Limnonectes paramacrodon				+
Megophryidae				
Megophrys nasuta				+
Leptobrachium abbotti			+	+
Leptolalax fritinniens				+
Microhylidae				
Chaperina fusca			**p**	
Kalophrynus cf. *barioensis*			+	
Kalophrynus meizon			**p**	
Kaloula baleata				**p**
Microhyla berdmorei				+
Microhyla petrigena			+	
Metaphrynella sundana			**c**	
Rhacophoridae				
Chiromantis inexpectatus			+	
Feihyla kajau			+	
Kurixalus appendiculatus			+	+
Nyctixalus pictus			**p**	
Philautus hosii		+		
Philautus nephophilus			+	
Polypedates leucomystax				+
Polypedates macrotis				+
Polypedates otilophus				+
Rhacophorus borneensis			**c**	
Rhacophorus cyanopunctatus			+	
Rhacophorus pardalis			+	+
Ranidae				
Amnirana nicobariensis				+
Abavorana luctuosa			+	
Chalcorana megalonesa	+	+		+
Huia cavitympanum			+	
Hylarana erythraea				+
Odorrana hosii		+		
Pulchrana picturata	+			+
Pulchrana signata			+	
Staurois guttatus	+	+		+
Staurois tuberilinguis			+	
Meristogenys orphnocnemis		+		+

Table 2. Updated species list for MBCA. See text for more details. + = recorded species; **c** = identification by call; **p** = photographic evidence.

Taxon	Ahmad and Wong (1998)	Lakim and Yambun (2002)	Traeholt et al. (2007)	Norhayati et al. (2010)	This study	Comments
Megophryidae:						
Megophrys nasuta	+		+		+	
Leptobrachium abbotti	+		+		+	
Leptobrachium montanum	+	+	+			
Leptolalax fritinniens		+	+		+	most likely as *L. gracilis* in Traeholt et al. (2007); *L. dringi* in Lakim and Yambun (2002)
Bufonidae						
Ansonia sp.	+		+		+	reported as *A. hanitschi* in these studies
Ansonia leptopus			+		+	
Ansonia longidigita	+	+			+	
Ansonia spinulifer		+	+		+	
Ingerophrynus divergens	+		+		+	*Bufo divergens* in previous accounts
Leptophryne borbonica			+		+	
Phrynoidis juxtasper	+	+	+	+	+	*Bufo juxtasper* in previous accounts
Rentapia hosii		+				*Pedostibes hosii* in Lakim and Yambun (2002)
Dicroglossidae:						
Fejervarya limnocharis		+			+	*Rana limnocharis* in previous accounts
Limnonectes finchi		+	+	+		*Rana finchi* in Traeholt et al. (2007)
Limnonectes ingeri					+	
Limnonectes sp. ("*kuhlii*") A	+	+	+	+	+	*Rana kuhlii* in Traeholt et al. (2007), *L. kuhlii* in the other reports
Limnonectes sp. ("*kuhlii*") B					+	
Limnonectes sp. ("*kuhlii*") C					+	
Limnonectes sp. ("*kuhlii*") D					+	
Limnonectes leporinus	+	+	+		+	*Rana blythi* in Ahmad and Wong (1998); *Rana leporina* in Traeholt et al. (2007)
Limnonectes palavanensis		+	+			*Rana palavanensis* in Traeholt et al. (2007)
Limnonectes paramacrodon					+	
Occidozyga baluensis			+			
Occidozyga sumatrana				**p**		
Ranidae:						
Amnirana nicobariensis		+	+		+	*Rana nicobariensis* in Traeholt et al. (2007), Lakim and Yambun (2002)
Abavorana luctuosa		+			+	*Rana luctuosa* in Lakim and Yambun (2002)
Chalcorana megalonesa		+	+		+	*Rana chalconota* in Traeholt et al. (2007), Lakim and Yambun (2002)
Huia cavitympanum		+	+		+	
Hylarana erythraea					+	
Odorrana hosii	+	+	+		+	*Rana hosii in* previous accounts
Pulchrana picturata		+	+		+	*Rana picturata* in previous accounts
Pulchrana signata	+				+	*Rana signata* in Ahmad and Wong (1998)
Staurois guttatus	+		+		+	*Staurois natator* in previous accounts
Staurois tuberilinguis	+				+	
Staurois latopalmatus		+				
Meristogenys orphnocnemis			+		+	*Meristogenys phaeomerus* in Traeholt et al. (2001)
Microhylidae:						
Chaperina fusca		+	+		**p**	
Glyphoglossus sp.	+					as *Calluella* sp. in Ahmad and Wong (1998)
Kaloula baleata		+			**p**	
Microhyla berdmorei	+				+	
Microhyla petrigena		+			+	
Kalophrynus cf. *barioensis*	+		+	+	+	most likely the same taxon as *Kalophrynus* sp. in Ahmad and Wong (1998) and *K. heterochirus* in Norhayati et al. 2010 and Traeholt et al. (2007)
Kalophrynus meizon					**p**	
Metaphrynella sundana	+	+		**c**	**c**	
Rhacophoridae:						
Feihyla kajau					+	
Chiromantis inexpectatus					+	Type locality (Matsui et al. 2014)

Taxon	Ahmad and Wong (1998)	Lakim and Yambun (2002)	Traeholt et al. (2007)	Norhayati et al. (2010)	This study	Comments
Kurixalus appendiculatus	+	+			+	*Rhacophorus appendiculatus* in previous accounts
Nyctixalus pictus				+	**p**	
Philautus aurantium			+	+		
Philautus hosii		+			+	
Philautus nephophilus					+	
Philautus larutensis				+		reported as *P. petersi*
Polypedates colletti	+					
Polypedates leucomystax		+	+	+	+	
Polypedates macrotis	+	+		+	+	
Polypedates otilophus		+	+		+	
Rhacophorus cyanopunctatus	+				+	*R. bimaculatus* in Ahmad and Wong (1998)
Rhacophorus borneensis					**c**	Type locality (Matsui et al. 2013b)
Rhacophorus gauni	+		+			
Rhacophorus harrissoni			+			
Rhacophorus pardalis	+		+		+	

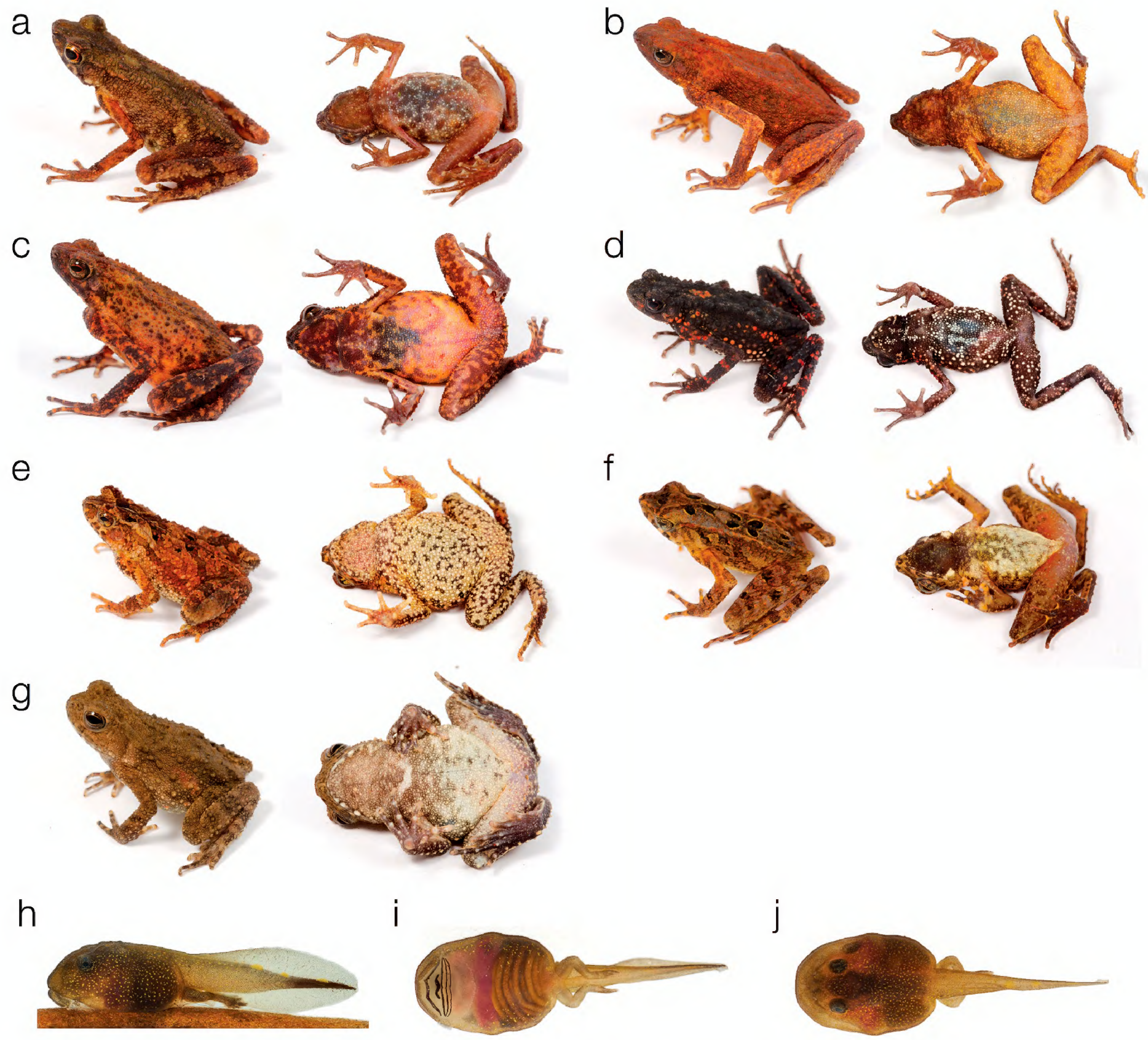

Figure 1. Frogs of the Bufonidae at MBCA: **a** Ansonia sp. ; **b**, *Ansonia leptopus*; **c**, *Ansonia longidigita*; **d**, *Ansonia spinulifer*; **e**, *Ingerophrynus divergens*; **f**, *Leptophryne borbonica*; **g**, *Phrynoidis juxtasper* (juvenile); **h–j**, *Phrynoidis juxtasper* tadpole (lot ZMH A12578) in lateral, ventral, and dorsal views. Images not to scale. Pairs of photos (dorsolateral and ventral) depict the same specimen.

Ansonia leptopus (Günther 1872): Brown Slender Toad; Fig. 1b

A slender toad, variable brownish in color, sometimes with tinges of orange; only faint color markings, indistinct crossbars on thigh and shank; small rounded warts on dorsum, larger flat warts at lateral dorsum and flanks; throat dark with lighter mottling; abdominal skin pebbled, mostly amber in color; snout projecting obliquely in lateral view; finger and toe tips rounded and slightly swollen; toes three-fourth webbed in males slightly less in female; no tarsal ridge; tympanum visible, small; iris golden with black network.—One female was recorded from a rocky tributary of Sungai Maliau. This species occurred in syntopy with *Leptolalax fritinniens*.

Ansonia longidigita Inger, 1960: Long-fingered Slender Toad; Fig. 1c

Snout obliquely protruding in lateral view; obtuse, rounded snout tip in lateral view; small conical warts on dorsum and dorsal side of limbs, often with small black spines giving a rough appearance; limbs and fingers long; almost uniformly brown to dark brown above, sometimes with reddish hue; diffuse scattered dark spots on the body; crossbars on thigh and shank may be indistinct in a dark marbled pattern; cream to amber with dark markings ventrally; darker on the throat and chest; toes and fingers bear rounded, slightly swollen tips; iris mostly golden to reddish-golden, with black reticulated pattern and thin reddish ring around pupil; tympanum distinct but small.—Two specimens were collected at the streams of Ginseng Camp, perching on low vegetation.

Ansonia spinulifer (Mocquard, 1890): Spiny Slender Toad; Fig. 1d

Snout obliquely protruding in lateral view; snout tip obtuse and rounded in lateral view; body generally slender; dorsum mostly black, with lighter yellowish or reddish warts laterally and in bands of such lighter warts on fore- and hind limbs; with a light cream, gray or reddish patch between shoulders; coarsely warted dorsally, warts with keratinized black spines; belly pebbled in texture, dark brown to black in color, with white markings; ventral side of thigh pebbled with scattered white spots; toes and fingers possess rounded, slightly swollen tips; iris black with some reddish stippling and a reddish ring around the horizontal pupil; tympanum distinct, vertically oval.—This species was common along the river at Ginseng Camp. Specimens were observed sitting on low vegetation close to the river. Encounters included numerous juvenile specimens along the Ginseng Camp stream below Ginseng Falls. One tadpole was captured at the river above Ginseng Fall.

Ingerophrynus divergens (Peters, 1871): Forest Toad; Fig. 1e

Body stocky; two hard ridges between eyes; parotoid gland narrow, longer than wide, posteriorly followed by row of warts; in general, coarsely warted above; warts pointed, with keratinized spinules; ventral skin coarsely pebbled in texture, cream with black spots in color; brown above with darker markings between eyes and on back; narrow vertebral stripe; limbs with cross bars ; sometimes with orange or reddish warts; ear drum visible but not different in color from surrounding skin; iris golden or reddish-gold with a black network.—*Ingerophrynus divergens* was common in the forest along Sungai Maliau and its tributaries and Agathis Camp. After rainfall, calling choruses of 10–20 males were encountered at some shallow, slow moving tributaries of Sungai Maliau.

Leptophryne borbonica (Tschudi, 1838): Cross Toad; Fig. 1f

A slender toad with long limbs, long fingers and toes; generally mid to dark brown above with various dark markings, particularly a diagnostic thick dark ‘X’-shaped mark, with cream contour line, on middle of dorsum and a less pronounced one on shoulder to head transition (in our specimen separated into distinct spots); lips with dark bars; belly cream with some dark markings; underside of thigh orange; parotoid glands narrow, elongated and indistinct, extending posteriorly into dorsolateral ridge of warts; iris golden (sometimes reddish in anterior and posterior sector of iris) with black reticulate pattern; ear drum indistinct in color and posteriorly covered by skin; slightly swollen finger and toe tips;—A juvenile was collected at Ginseng Camp, along the rocky stream above Ginseng Falls, perching on low vegetation.

Phrynoidis juxtasper (Inger, 1964): Giant River Toad; Fig. 1g

A large and stocky toad; with large, prominent parotoid gland behind eye; large warts all over the dorsal side; warts rounded to conical, bearing spinule; dorsal coloration uniformly grayish to mud brown; dark markings present or absent; ear drum small and indistinct; iris, golden with fine, dark reticulation—*Phrynoidis juxtasper* is common along Sungai Maliau, however, calling activities sightings of adults were low during the survey. Apart from Sungai Maliau, the species was also present at Nepenthes and Agathis Camp.

To our knowledge, photos of *P. juxtasper* tadpoles have only been published for Sumatra (Manthey and Grossmann 1997:32). Larvae from Sungai Maliau (Fig. 1h–j) were collected in quiet, shallow (< 20 cm) shore waters among rocks. One tadpole (ZMH A12647) was barcoded (accession: MG909569) to exclude erroneous

assignment to *P. asper*. The tadpole body is ovoid in dorsal view, widest behind eyes, and slightly depressed dorsoventrally. The snout is short and a steeply inclined slope in lateral view. The eyes are dorsolateral in position. The tail is short, comprising only approx. 55% of total length. The coloration is generally dark brown above with plenty of yellow dots. The tail is less dark than the body; it bears 2–3 bright yellow spots along the upper edge of the tail's muscular part. The tail fin is weakly pigmented and moderately high; the tail tip is broadly rounded, blunt. Two keratodont rows are present on the upper lip, three on the lower lip. Lips are broadly expanded to form a sucker mouth. The ventral side is mostly transparent. The gut is arranged in a conspicuously transversely oriented coil. Metamorphs and juveniles were encountered in large numbers along Sungai Maliau and slightly larger juveniles along the Maliau tributaries, respectively. The presence of larvae, juveniles, and slightly larger juveniles at distance from Sungai Maliau suggested that a major breeding event had occurred most likely in December/January and juveniles were migrating into the forest.

Dicroglossidae, Fanged Frogs

Fejervarya limnocharis (Gravenhorst, 1829): Grass Frog; Fig. 2a

Body slender to stocky; narrowing snout in dorsal view; snout projecting well beyond lower jaw in lateral view; finger and toe tips not expanded; prominent broken longitudinal ridges on back; coloration from shades of gray to brown and greenish hues, with scattered dark blotches; often with vertebral stripe; alternating light and dark marks across lips; belly white or cream underside of hind limb flesh colored; males with dark throat markings; ear drum moderately distinct; iris brass in the upper sector, silvery in the lower; outside the iris the eye bulb is white-bluish.—*Fejervarya limnocharis* is not a true forest species, although it may occur at clearings. It is present in rural areas such as rice paddies, road ditches, or ponds and puddles logged areas. It is common at puddles and swampy areas of the Study Center and ditches along the road to Belian Camp.

Limnonectes ingeri (Kiew, 1978); Fig. 2b

A large, heavy frog with muscular, long legs; area between nostril and eye smooth, not forming an edge (i.e., no canthus rostralis); head broad and flat; finger and toe tips slightly bulbous but not expanded; toes fully webbed; dorsal skin finely textured, shagreened, with scattered tubercles and small ridges; multiple conical tubercles on top of the eye; supratympanic fold long, with black line, bending in angled manner around tympanum to shoulder; tympanum moderately distinct (colored as surrounding skin); color homogeneously brown above; some black blotches posterior to shoulder; sometimes red on thigh; dark markings on upper and lower lip; a thin mid-line cream colored streak can be present or absent; thin banding on thigh; venter white, dotted brown, throat dark mottled; thighs pale with some cream spots; iris densely stippled silver-gold on black background, venation pattern.—This large species was encountered in the riparian habitat along Sungai Maliau, from one of its tributaries.

Limnonectes sp. Creek Frog complex; Fig. 2c

Although the Creek Frog species complex (formerly known as *L. kuhlii*) consists of a multitude of species (McLeod 2010, Matsui et al. 2016), a general short description can be given: SVL to 88 mm in males; robust frogs with very muscular thighs; fully or partially webbed toes; eyes more upward directed than in other species; skin with conspicuous reticulate, polygonal pattern of small ridges above; rough tubercles may be present on upper side of shank and thigh; color above with ochre to mid-brown background and extensive dark brown to olive-brown blotches; broad bands on arms and legs; belly white to cream with mottling laterally and on chest and throat; finger and toe tips slightly swollen; distal phalanx of toes sharp and can penetrate the skin for defense against predators; ear drum invisible; iris silver-gold to brown, with four dark radials; odontoid processes on anterior of lower jaw.—The taxonomy of the frogs formerly known as *L. kuhlii* is in a state of taxonomic transition because it has been demonstrated that *L. kuhlii*, in fact, is a species complex of similar frogs consisting of many species in Sabah and Sarawak (McLeod 2010, Matsui et al. 2016) covering a wide range of body sizes (Kueh et al. 2010b). New species names have not been proposed yet for many of the genetically well-delimited lineages and, thus, we list the barcoded frogs from our survey in The Appendix 1: Specimen vouchers section under the respective clade number from Matsui et al. (2016) that they matched best genetically. Specimens from this species complex where recorded at Sungai Maliau tributaries, Agathis Camp and Ginseng Camp streams. According to a preliminary comparisons using sequence data of Matsui et al. (2016) our samples represent Matsui et al. (2016) Lineages 2, 5, 12, and 17.

Limnonectes leporinus (Andersson, 1923): Giant River Frog; Fig. 2d

Robust large frog with strong hind limbs and broad triangular head; snout long and tapering in dorsal view, projecting well beyond lower jaw in lateral view; mostly smooth, dorsal skin texture shagreened, occasionally with scattered elongated tubercles and short ridges on back, esp. in juveniles; tubercles on top of eye; toes fully webbed; grayish, sandy brown to mid-brown above with scattered dark spots; dark band between eyes; dark streak from eye to snout along an edge between eye and nostril (canthus rostralis); dark markings on lips; dark below supratympanic fold and upper part of ear drum; supratympanic fold being in a moderate angular manner around tympanum; tympanum moderate-

Figure 2. Frogs of the Dicroglossidae and Megophryidae at MBCA: **a**, *Fejervarya limnocharis*; **b**, *Limnonectes ingeri*; **c**, *L. kuhlii*; **d**, *L. leporinus*; **e**, *L. paramacrodon*; **f**, *Leptobrachium abbotti*; **g**, *Leptolalax fritinniens*; **h**, *Megophrys nasuta*. Images not to scale. Pairs of photos (dorsolateral and ventral) depict the same individual.

ly distinct; hind limb barred above; belly uniform cream; throat faintly mottled; odontoid processes on anterior of lower jaw; iris golden with three more or less pronounced dark radial areas (anterior, posterior and ventral sectors) and fine black venation.—This large river frog is common along lowland rivers of Sabah and Sarawak and was detected at the Sungai Maliau tributaries, Ginseng and Agathis Camps. Often these frogs sit on the ground of the river bank a few meters from the water line. One male was observed building a nesting site, i.e., a circular depression in the fine gravel of one of Sungai Maliau's tributaries. The male was calling with a deep single note and a female was noticed nearby.

Limnonectes paramacrodon (Inger, 1966): Lesser Swamp Frog; Fig. 2e

Snout long and tapering in dorsal view; bulging bluntly beyond lower jaw in lateral view; toe tips slightly widened, finger tips rounded and not widened; toes webbed to almost the tip, except for Toe IV; webbing; dorsal side sandy brown, mid-brown or reddish brown, uniform or with irregular markings; supratympanic fold bending around tympanum; tympanum almost entirely covered with dark fleck below supratympanic fold; dark streak from eye to nostril along canthus rostralis; contrasty light and dark markings on upper and lower lips; faint banding on thigh; venter yellowish; throat mottled; dorsal skin texture shagreened with some low tubercles and short ridges on back; odontoid processes on anterior of lower jaw; iris golden with four conspicuous dark radials and fine black venation;—*L. paramacrodon* was common in the riparian habitat of Sungai Maliau. Numerous juveniles were encountered at swampy areas in the forest along Belian and Wildlife trails near the Study Center, suggesting that this species might use these swampy areas for reproduction.

Megophryidae, Leaf-litter Frogs

Leptobrachium abbotti (Cochran, 1926): Lowland Leaf-litter Frog; Fig. 2f

Limbs slender; head wider than body; eyes large; toes nearly free of webbing; hind limbs relatively short; fore-

limbs long and thin; supratympanic fold arched around ear drum; upper part of tympanum with a dark mask; skin of dorsum smooth to granulated; dark brown above, with a darker pattern on forehead; ventral side smooth; abdominal skin dark grayish with white spots partially arranged in rows; throat white with grayish markings; iris dark brown to black; beyond the iris the eye is blueish.—The species was present on the forest floor along Sungai Maliau (Wildlife Trail) and at Nepenthes Camp. A calling chorus of this species was noticed at Agathis Camp.

Leptolalax fritinniens Dehling & Matsui, 2013: Twittering Slender Litter Frog; Fig. 2g

Snout rounded; vocal sacs of males subgular and bipartite; supratympanic fold angled; tympanum distinct, dark; venter white with darker blotches; generally grayish or brownish to anthrazite above with some light brown flecks and large dark blotches; blotches and flecks not bordered in light color; dorsal surface of upper arm and part of hind limb lightened; thigh with distinct banding; iris grayish with reddish sector dorsally and red iris edge around pupil.—Calling males were detected along a tributary right of Sungai Maliau. This side stream was rocky and had large boulders. Males perched on low vegetation (< 50 cm) up to 10 m away from the waterline, elevated on the steep river banks.

Megophrys nasuta (Schlegel, 1858): Bornean Horned Frog; Fig. 2h

Body robust, particularly in females; relatively short hind limbs; head large, wider than long; prominent triangular, dermal appendages on tip of snout and upper eyelids; ear drum hidden; two pairs of parallel dermal folds on back; dorsal skin mostly smooth with scattered tubercles, some of the conical; tips of fingers and toes rounded, not expanded; toes webbed at base; dorsum brown with darker markings; a dark bar from eye to upper lip; limbs with narrow crossbars; throat reddish-brown to dark brown in males; posterior half of ventral side whitish with dark flecks; iris dark brown to reddish brown, somewhat lighter in upper part.—The species was not active at the time of our survey. One specimen was encountered near Study Center, Belian Trail.

Microhylidae, Narrow-mouthed Frogs

Chaperina fusca, Mocquard, 1892: Saffron-bellied frog, Fig. 3a

SVL up to 24 mm, males smaller; moderately slender body with long hind-limbs; head narrower than body, with rounded short snout; finger and toe tips slightly widened, without webbing; a tiny whitish skin spur is located at each elbow and heel; dorsal skin structure smoothly pebbled, venter smooth, small tubercles on upper side of hind limb; dorsum mottled grayish on dark brown background; upper side of limbs brown with dark brown bands or markings; white dots laterally and on limbs; ventral side with large, bright yellow spots; tympanum visible but indistinct; pupil elliptical and horizontal; iris black with golden stippling.—The species was observed and photographed at Nepenthes Camp but likely is not restricted to the MBCA southern plateau. No specimen was collected.

Microhyla berdmorei (Blyth, 1856): Berdmore's Narrow-mouthed Frog, Fig. 3b

Broad flat body with long hind limbs; snout contour in dorsal view tapering but narrowly rounded; finger tips moderately widened, toe tips clearly widened into discs, somewhat truncated digital discs; fully webbed toes, except for fourth toe; dorsal skin texture relatively smooth, with scattered fine tubercles; color brown above, with dark and light-edged polygonal marking from shoulder to mid-back; banding pattern on limbs; venter yellow, ventral side of limbs dull yellow; throat dark and finely mottled brown; iris brass with dark reticulate pattern; ear drum invisible;—This microhylid ground-dwelling species was encountered at and around swampy areas and roadside ditches along Belian Trail.

Microhyla petrigena (Inger & Frogner, 1979): Pothole Narrow-mouthed Frog, Fig. 3c

SVL up to 18 mm; short, stocky body; long hind limbs relative to body; narrow, small head; snout short; skin mostly smooth with fine tuberculation; only three fingers present; finger and toe tips expanded, blunt; toes fully webbed except for fourth toe; general color in shades of brown above (including ochre, chocolate and reddish tones); finely mottled, larger dark markings at flanks, at anus and at thighs are outlined with light edges; dark marking central on back, constricted just behind shoulder level and expanding posteriorly; light stripe from eye to shoulder joint; ventral side mostly chocolate with conspicuous white blotches; ear drum invisible under skin; iris finely stippled silver to brass on black background, with orange ring around pupil.—This small species was recorded from a stagnant forest pool near Nepenthes Camp. It is tentatively assigned to *M. petrigena* based on the reduced first finger and white marking on the belly (also following mentioning in Matsui et al. (2014) from the same locality). The specimens were found near a stagnant forest pool, although *M. petrigena* typically has been reported breeding in potholes of rocky streams (Inger et al. 2017).

Kalophrynus cf. *barioensis* Matsui & Nishikawa, 2011: Bario Sticky Frog, Fig. 3d

Stocky, broad, flat body, short limbs; narrow head relative to body, short pointed snout; all fingers short except third; outer finger and toe very short, nub-like; webbing

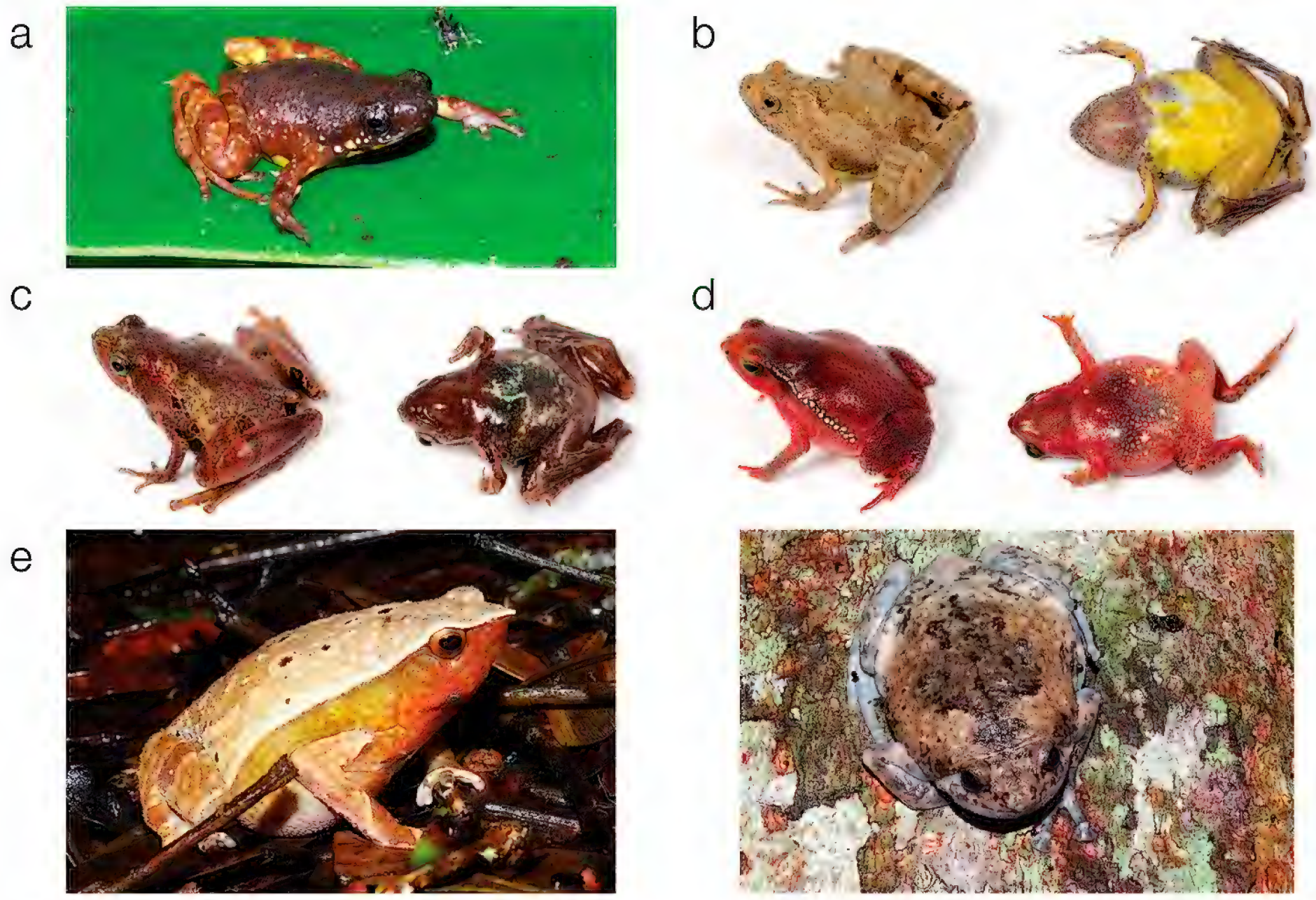

Figure 3. Frogs of the Microhylidae at MBCA: **a**, *Chaperina fusca* (photo voucher only); **b**, *Microhyla berdmorei*; **c**, *Microhyla petrigena*; **d**, *Kalophrynus* cf. *barioensis*; e, *Kalophrynus meizon* (photo voucher only); f, *Kaloula baleata* (photo voucher only). Images not to scale. Pairs of photos (dorsolateral and ventral) depict the same individual.

reduced; dorsal skin texture granulated to moderately tuberculate; color red-brown above, with faint dark markings; toes and fingers bright orange to red; inguinal spot light colored and distinctly edged dark; row of well-defined cream tubercles from above ear drum towards groin; dark-edged cream inguinal spot; similar smaller spots on rear of thigh; iris bronze with fine reticulate pattern; pupil horizontal; ear drum indistinct.—The species was tentatively assigned to *K. barioensis* based on 98% similarity with sequence KM509147.1 from GenBank, despite deviation from the original description of *K. barioensis* in inguinal spot color, thigh pattern, and dorsal color. The species was found to be abundant in the heath forests (*Kerangas*) of the Maliau Southern Plateau. Males call during the day from the forest leaf litter away from water (in accord with the original description of *K. barioensis*; Matsui and Nishikawa 2011). Preliminary evidence suggests that this species is a phytotelm breeder using *Nepenthes* pitchers to deposit eggs (Ahmad and Wong 1998).

Kalophrynus meizon Zug, 2015: Borneo Big Sticky Frog, Fig. 3e

Body stocky, head small in relation to body, snout pointed but short; limbs moderately long; finger and toe tips not expanded, third finger conspicuously long; toe webbing variable, approx. half of toes; dorsal skin structure finely pebbled in females, finely spinose in males; dorsal skin color sand to brown often with darker markings and black spots; a narrow light line from snout tip to groin separates the dorsum from the darker or orange flanks; dark spot in groin region; abdomen light gray, throat orange to rusty; pupil horizontal, iris gold-brown.—The species was recorded by photograph for Nepenthes Camp; no specimen was collected.

Kaloula baleata (Müller, 1836): Brown Bullfrog, Fig. 3f

Body squat and clumsy; hind limbs relatively short; head significantly narrower than body, snout short, eyes relatively small; tympanum invisible; fingers and toes long, distally expanded, toes more so; toe webbed at base; dorsal skin granular with scattered tubercles; even lower jaw with rough skin; dorsal skin coloration quite variable, usually marbled in shades of brown and gray, often darker in central part of dorsum; pupil elliptical, horizontal in orientation; iris dark amber.—The species is mostly seen during breeding activities when the loud deep calls of the males can be heard. The specimen in Fig. 5b was photographed near Study Center; no specimens were collected.

Metaphrynella sundana (Peters, 1867): Tree Hole Narrow-mouthed Frog

Short, narrow, somewhat obtuse snout; toes and fingers relatively large, fleshy, and bear expanded digital discs; toes webbed half; dorsal skin texture warty; color mostly brown and gray, variable pattern but commonly with a large dark constricted marking on the dorsum; fingers and toes often with yellowish or orange; iris black with some bronze stippling; pupil horizontal; ear drum rather indistinct.—*M. sundana* was present in the forests of the Southern Plateau. Reproductively active males called from tree-holes, some of them several meters above ground. Account by acoustic identification, no photo vouchers, none collected.

Ranidae, True Frogs

Amnirana nicobariensis (Stoliczka, 1870): Cricket Frog; Fig. 4a

Slender body; head long and narrow; long hind limbs with great jumping performance; fingers and toes elongate and with slightly swollen tips; toes half webbed; long snout, pointed in dorsal view; snout projecting lower jaw, narrowly rounded in lateral view; dorsal skin texture finely pebbled or granulated; dorsal side uniform mid-brown to marbled brown; dorsal side of hind limbs with darker bars; black streak at side of head starts from snout, broadens to band under canthus rostralis and continues behind eye covering the ear drum and beyond; dorsolateral fold present, thin but continuous from eye to pelvic region; tympanum large and distinct; upper lip als uniform white streak that continues onto rictal ridge behind jaw joint; venter cream, throat cream with darker mottling; thighs in pale flesh color below and weak banding above; iris dark reddish-brown below, golden above.—This species commonly follows human alteration of landscapes such as rural areas, road ditches and clearings; it does not enter the forest. At Maliau Basin it is present in large numbers at the pond of the Study Center and in ditches along the roads.

Abavorana luctuosa (Peters, 1871): Mahogany Frog; Fig. 4b

Moderately stocky with moderately long limbs; toes webbed to less than half of their length; finger and toe tips slightly expanded, narrowed to the tip; snout protruding beyond lower jaw and rounded in lateral view; area between eye and nostril smooth; skin texture smooth; a mahogany-brown area is delimited by a circumferential thin white to orange line on the dorsum and head; cream streak on upper lip from under the eye to shoulder; remaining parts of body mostly black; arms and legs variable, with black banding on brown background or black with banding in light gray; flanks gray with or without black dots; tympanum large and distinct; under side dark gray with white spots on venter and vermiculated pattern on thighs, zebra pattern on underside of shank; webbing; ear drum black, distinct, and large; iris dark brown to black, except for golden upper fifth;—The species was present with adults and larvae in a pond near Nepenthes camp. For size and altitudinal range see Kueh et al (2010a).

Chalcorana megalonesa Inger, Stuart & Iskandar, 2009: Large White-lipped Frog; Fig. 4c

A relatively large species in the genus; body slender; limbs, fingers, and toes long; head long and narrow; snout pointed; snout projects with sharp tip beyond lower jaw in lateral view; snout longer than eye diameter; canthus rostralis present; fingers and toes long, bearing significantly expanded tips in form of adhesive disks with circummarginal grooves; tympanum very distinct and large (in males); dorsal skin texture finely granular; brown above with scattered dark spots; flanks often green otherwise brown; upper lip all cream in color, cream streak extends beyond jaw joint to shoulder; ventral side cream on venter and throat; under side of thighs flesh colored; iris golden with fine black venation and more reddish hues in anterior and posterior sectors.—*Chalcorana megalonesa* is a common sighting at the Study Center, Sungai Maliau tributaries, Agathis river and streams, and Ginseng Camp streams. Early stage tadpoles were present (not collected) in an isolated side puddle of one of the Sungai Maliau side streams.

Huia cavitympanum (Boulenger, 1893): Hole-in-the-head Frog; Fig. 4d

Body moderately stocky but with strong and long hind limbs; toes and fingers with terminal expanded and slightly pointed discs; toes fully webbed; dorsal skin texture mostly smooth, flanks with low tuberculation; color dark brown on dorsum, separated from lighter flank by ochre to orange dorsolateral stripe; dorsolateral fold broken; dark blotches expand from eye posteriorly, ventrally and anteriorly; hind limbs distinctly banded; ochre to orange line along upper side of shank; ventral side uniform yellow; tympanum distinct but small, sunken in, transparent; iris bicolored, dark reddish-brown below and beige to golden in the upper third.—The species has large tadpoles that are highly adapted to fast currents. The tadpoles can hold on to rocks in very fast currents by applying their conspicuous abdominal sucker. Because of this larval adaptation, this species is linked to clear cascading streams, however, individuals can occasionally be found at some distance from the stream. We recorded the species from the Fawzy Waterfall area.

Hylarana erythraea (Schlegel, 1837): Green Paddy Frog; Fig. 4e

Body moderately robust with long and muscular hind limbs; head and snout relatively long and moderately

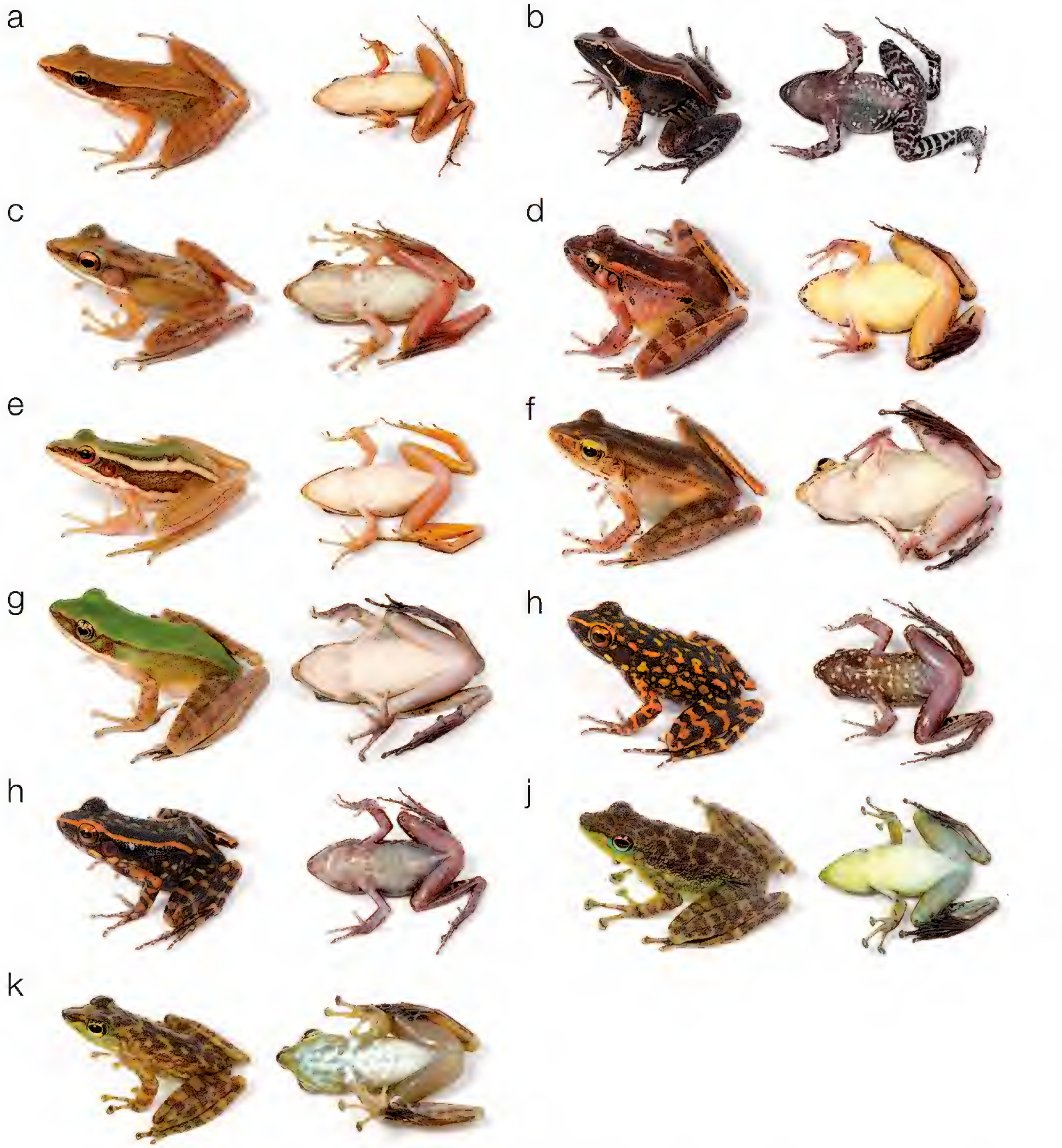

Figure 4. Frogs of the Ranidae at MBCA: **a**, *Amnirana nicobariensis*; **b**, *Abavorana luctuosa*; **c**, *Chalcorana megalonesa*; **d**, *Huia cavitympanum*; **e**, *Hylarana erythraea*; **f**, *Meristogenys orphnocnemis*; **g**, *Odorrana hosii*; **h**, *Pulchrana picturata*; **i**, *Pulchrana signata*; **j**, *Staurois guttatus*; **k**,*Staurois tuberilinguis*. Pairs of photos (dorsolateral and ventral) depict the same individual.

narrow; finger and toe tips only moderately expanded to rounded discs; toes webbed to half; dorsal skin texture smooth to granular, areolate at the flanks; color predominantly green above; dorsolateral fold thick, continuous and cream in color, bordered in dark brown; upper lip cream without marking; upper lip streak continues posteriorly in a lower longitudinal stripe at lower flank; upper side of limbs sandy brown; throat, chest and abdomen ventrally all white; thighs flesh to orange in color tympanum conspicuous, large, dark in color; iris golden in upper part, darker below, with dark mid-horizontal band.—At Maliau, the species is abundant at the Study Center Laguna and roadside ditches. *H. erythraea* and *A. nicobariensis* frequently occur together in many Bornean rural water bodies, such as village ponds and paddy fields.

Meristogenys orphnocnemis (Matsui, 1986): Northern Torrent Frog, Fig. 4f

Slender (males) to moderately stocky (females) body with long slender legs; snout moderately long; tips of toes and fingers expanded, slightly rhomboidal; toes fully webbed; skin texture finely shagreened; dorsolateral fold present; color above brown, with scattered dark dots and light markings; upper lip without dark markings; upper side of thigh broadly banded; throat, chest and belly white or cream; males with lateral dark vocal sack areas on throat; rear of thigh mottled dark with light spots; iris golden in upper and lower sectors, reddish in anterior and posterior sectors. —*Meristogenys orphnocnemis* was most common at Ginseng Camp streams, but also recorded at one of the larger, rocky Sungai Maliau tributaries. Most often individuals of this species perched on roots, rocks or the soil at the slopes of the stream banks. The species identity was confirmed by genetic barcoding and matching to previously published data (Matsui et al. 2006, Shimada et al. 2011a,b). Tadpoles were found at night while adhering to rock surfaces at a stream next to Ginseng Camp. Tadpole identification followed the key in Shimada et al. (2015).

Odorrana hosii (Boulenger, 1891): Poisonous Rock Frog; Fig. 4g

Body moderately robust with long and muscular hind limbs; toes and fingers long; tips of fingers and toes expanded to large rhomboidal discs; toes fully webbed; webbing dark in color; dorsal skin texture shagreened to granulated; ventral skin texture smooth anteriorly but areolate on posterior belly and thigh; color mostly green above, flanks can be brown; dorsolateral fold present but weakly developed, set off by dark line; upper side of limbs green or brown, with banding; dark stripe from nostril to eye along canthus rostralis; upper lip cream without markings, cream stripe continues to shoulder; ventral side white; tympanum distinct, dark in color, moderate in size; iris silver to gold in upper and lower part with abundant black reticulating pattern, mostly black in anterior and posterior part, with narrow golden ring around pupil,—*Odorrana hosii* was found at the rocky stream below Ginseng Falls perching high up the steep banks.

Pulchrana picturata (Boulenger, 1920): Spotted Stream Frog; Fig. 4h

Body slender to moderately robust; limbs moderately long; head relatively narrow, moderately long snout; tips of digits slightly swollen; webbing to approximately half the toes; granular dorsal skin texture; color black with yellow to red spots and angular blotches; colored line from snout to eye and along upper eye lid; no continuous stripe from eye to groin; banded pattern on upper side of limbs; venter dark gray with scattered cream spots; tympanum distinct, black; iris coppery, with reddish narrow ring around pupil and abundant black reticulate pattern.—This species prefers rocky streams. It occurs at the Sungai Maliau tributaries, Agathis Camp and Ginseng Camp; however, the species was not abundant during our survey. *Pulchrana picturata* and *P. signata* belong to a species complex that has not been fully resolved yet on the island of Borneo.

Pulchrana signata (Günther, 1872): Striped Stream Frog; Fig. 4i

Body slender to moderately robust; limbs moderately long; head relatively narrow, moderately long snout; tips of digits slightly swollen; webbing to approximately half the toes; granular dorsal skin texture; color black with yellow to red angular spots or blotches; colored line from snout to eye, along upper eye lid and posterior to groin; banded pattern on upper side of limbs; venter gray, thigh darker; tympanum distinct, blackish; iris coppery, with reddish narrow ring around pupil and abundant black reticulate pattern.—*Pulchrana picturata* and *P. signata* belong to a species complex that has not been fully resolved yet on the island of Borneo. The specimen reported here was found at a forest pond near Nepenthes Camp.

Staurois guttatus (Günther, 1858): Black-spotted Rock Frog, Fig. 4j

Body slender; snout long, pointed and protruding in lateral view; long fingers and toes, tips of digits broadly expanded; webbing of toes shiny turquoise blue; upper head and back yellowish brown to olive brown with dark spots on back, light green or yellowish green at the flanks with white dots; limbs brown to green above with more or less pronounced dark banding; lips without bars; outer third of digital discs with light cross band; dorsal skin texture pebbled or slightly warty, especially dorsolaterally; ear drum distinct but small; ventral side of throat, breast and belly white, more yellowish anteriorly; underside of limbs not white but greenish gray; iris gold to copper in upper sector, black in anterior and posterior sector and pale silvery in lower sector, narrow color ring around pupil (copper except for lower pale silver sector).—*Staurois guttatus* is a common species along medium sized streams of Maliau. It was quite abundant at the Sungai Maliau side streams, Agathis Camp and Ginseng Camp. Individuals typically perched on low vegetation (< 150 cm) along the bank of streams or on vegetation growing among boulders in the stream.

Staurois tuberilinguis (Boulenger, 1918): Green-spotted Rock Frog, Fig 4k

Body slender; snout long, narrow, edged, pointed and protruding in lateral view; long fingers and toes, tips of digits

broadly expanded; webbing of toes shiny turquoise blue; upper head and back yellowish brown to olive brown with dark spots on back forming marbling, flanks not sharply different from back; limbs brown to olive brown above with distinct dark banding; lips without bars; outer third of digital discs with light cross band; dorsal skin texture pebbled, tuberculate on flank; scattered short longitudinal ridges on dorsum and flank; ear drum distinct but small; ventral side of throat, breast and anterior belly white with diffuse dark spots; underside of limbs not white but brown to gray; iris golden in upper sector, black in anterior and posterior sector and pale golden in lower sector, narrow gold ring around pupil.—The species was abundant at Fawzy Waterfall. The species was distinguished from *S. parvus* by overall size (Matsui et al. 2007)

Rhacophoridae, Asian Tree Frogs

Feihyla kajau (Dring, 1983): White-eared Tree Frog, Fig. 5a

Slender body; snout very short and blunt, eyes slightly forward directed; finger and toe tips broadly rounded; webbing at base of outer fingers; toes half-webbed; dorsal skin texture finely shagreened; wavy edge along outer border of fourth finger and forearm and outer foot; color green above abruptly ending at flanks, brown posteriorly (pelvic region), scattered white dots above; venter white anteriorly and transparent posteriorly; iris silvery below and golden above, with some dark reticulation and golden ring around pupil; pupil horizontally oval; ear drum present but small and inconspicuous due to coloration of skin.—A number of individuals of *F. kajau* were found at a small forest stream with pools of low flow velocity. The stream is crossed by the trail from Fawzy Waterfall to Nepenthes Camp.

Chiromantis inexpectatus Matsui, Shimada & Sudin, 2014: Bornean Opposite-fingered Tree Frog, Fig. 5b

Body slender with relatively long fore limbs; head wide and flat; snout short; eyes slightly forward directed; outer fingers webbed at base; toe and finger tips expanded to adhesive discs; dorsal skin texture smooth, venter smooth; color yellow to brown above with dark spots; venter semi-transparent pink or red, with two longitudinal white streaks; brown band runs from tip of snout to flank at half of body, adjoined below by a cream stripe; iris amber, fading into beige at the dorsal and ventral periphery; eye moderately large; pupil without distinctly colored edge; pupil oval horizontally; ear drum present, small, inconspicuous.—This small rhacophorid species was described by Matsui et al. (2014), who collected the species in 2005. We confirm its presence at the type locality, an oblong forest pool of moderate depth. Individuals perched 1–3 m high on vegetation close to the pool. Males were observed to call from above and under leaves.

Intensive dip-netting of the pool revealed one *Chiromantis inexpectatus* tadpole. Barcoding the tadpole (ZMH A12597; Genbank accession MG909568) resulted in a 99% match with previously existing sequences (AB813160.1). The single specimen does not allow a full description of the tadpole features because of early stage (Stage 25), and damage inflicted during capture. We present here the first image of the tadpole of this species, as confirmed by genetic match with adults (Fig. 5c). The individual is 15 mm long with the tail 60.7% of the total length (tail tip damaged). The body shape in dorsal view resembles a strongly rounded rectangle. The eyes are lateral in position (cornea extend beyond body contour in dorsal view). The body is strongly pigmented with conspicuous bright white spots at the snout and dorsolaterally at the head-trunk transition. The tail is much less pigmented than the body.

Kurixalus appendiculatus (Günther, 1858): Frilled Tree Frog, Fig. 5d

Body slender; head relatively broad, triangular; snout pointed, females with pronounced snout projection; finger and toe tips broadly expanded into adhesive discs; toes webbed to three-fourth; outer fingers webbed at base; forearm and foot bear a wavy fringe of skin along outer side; series of skin projections ventrally along mandible; dorsal skin texture irregular, tuberculate; venter skin texture distinctly areolate; color above can combine brown, gray, and green with various markings, highly variable, resembling bark; throat and venter cream, ventral side of legs gray to brown; eyes large; pupil oval horizontally; iris color gold, often paler around pupil and in lower part; iris moderately reticulated; ear drum small, distinct but not set off in color from surrounding skin.—The species is probably widespread in the Maliau Basin. We encountered it in the low elevation swampy habitats at the Belian Trail areas as well as the more elevated forests around Nepenthes Camp. Males prefer to stay close to muddy forest floor depressions and often call even if such sites are not water-filled. An adult female was found at night close to the trail from Nepenthes Camp to Fawzy Waterfall sitting low on a bush.

Nyctixalus pictus (Peters, 1871) Cinnamon Frog, Fig. 5e

Medium sized, slender frog; head relatively wide, triangular and flat, snout long; canthus rostralis edged; hind limbs long; toes and finger bear round expanded discs, each disc bears two white dots; toes approximately half-webbed; dorsal skin structure spinose, spines low; dorsal coloration reddish-brown to orange, skin spines may be pale; white dots scattered over dorsal surface, flanks, and limbs; a row of white spots from snout tip to eye and along edge of upper palpebra; tympanum visible, large; eyes large; pupil rhomboid; iris white in upper

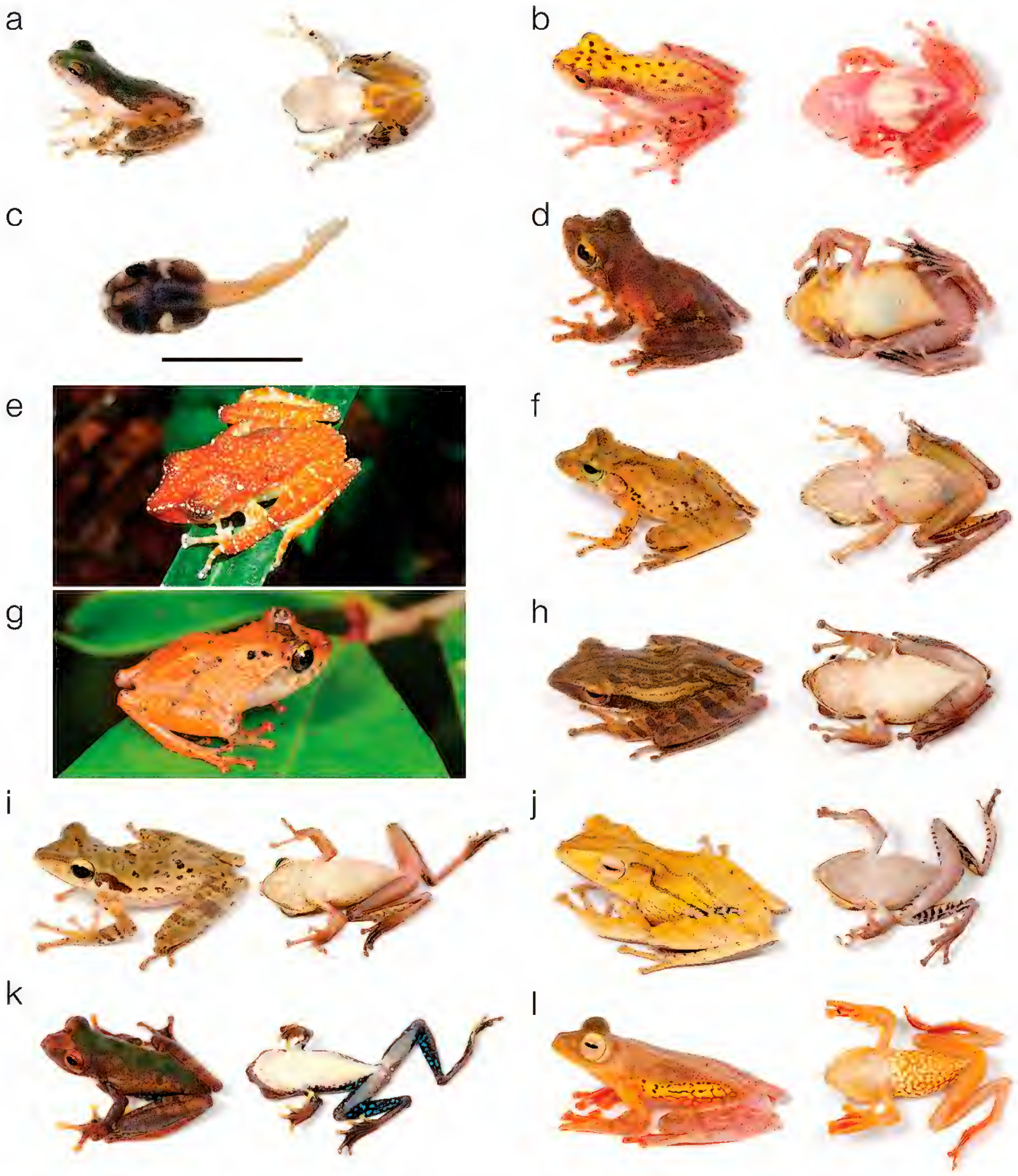

Figure 5. Rhacophorid frogs at MBCA: **a**, *Feihyla kajau*; **b**, *Chiromantis inexpectatus*; **c**, *Chiromantis inexpectatus* tadpole, scale: 5 mm; **d**, *Kurixalus appendiculatus*; **e**, *Nyctixalus pictus* (photo voucher only); **f**, *Philautus hosii*; **g**, *Philautus nephophilus*; **h**, *Polypedates leucomystax*; **i**, *Polypedates macrotis*; **j**, *Polypedates otilophus*; **k**, *Rhacophorus cyanopunctatus*; **l**, *Rhacophorus pardalis.* Pairs of photos (dorsolateral and ventral) depict the same individual.

sector, red in anterior, posterior, and lower sectors.— The specimen reported (photographic evidence) here was encountered at Nepenthes Camp. The species is a treehole breeder and, thus, independent of streams or ponds and might be widely distributed at MCBA. No specimen was collected.

Philautus hosii (Boulenger, 1895): Hose's Bush Frog, Fig. 5f

Body moderately stout; head flat and broad, large eyes; snout long; canthus rostralis edged; toe and finger tips broadly expanded into adhesive discs; toes almost fully

webbed; dorsal skin texture granulated, with some tubercules; tubercles can form V-shape on shoulder; skin of venter areolate; color above sandy to mid brown often with faint dark X-marking on back; scattered black spots, particularly from arm pit posteriorly; some banding on limbs; ventral side cream with pale gray-brown areas peripherally; ventral side of thighs darker, not cream; dorsolateral fold absent, supratympanic fold present, bent towards armpit and edged with dark pigmentation; iris color usually with a distinct green hue and with fine black venation; pupil horizontal, thinly edged with golden line; ear drum distinct but not set off from surrounding skin in color or skin texture.—*P. hosii* is a large *Philautus* and generally a common frog. It is most easily recognized by it's distinctive call; males often sit several meters high in trees and can be hard to spot.

Philautus nephophilus (Dehling, Matsui & Yambun, 2016): Bush Frog 5g

Body relatively stout, but with long hind limbs; head relatively broad; snout and lower jaw arch broadly rounded; toe and finger tips expanded into adhesive discs; toes half-webbed; dorsal skin texture moderately tuberculate and granulated; dorsal color variable from olive to shades of brown with dark markings; some with X-shape pattern on mid-dorsum; limbs with banding; venter coloration brown; iris coloration golden in the dorsal sector, paler, more silvery in the lower sector and dark brown in the anterior and posterior sectors; ear drum concealed by skin.—This small species of *Philautus* was common around Nepenthes Camp. Among the genus, 16S data from MBCA specimens clustered closest with the 16S data provided in the original description of *P. nephophilus* from Kinabalu (Dehling et al. 2016, p-distance 2.5%). We regard this mild divergence (97,5% similarity) a result of isolation by distance between conspecific populations of *P. nephophilus* following the rationale proposed by Vences et al. (2005a, b).

Polypedates leucomystax (Gravenhorst, 1829): Four-lined Tree Frog, Fig. 5h

Body slender with long hind limbs; head relatively broad and triangular; sharp canthus rostralis; toes and fingers expanded into near circular, slightly blunt discs; toes fully webbed, except fourth; dorsal skin texture smooth (lack of tubercles) but finely granulate; ventral skin areolate; supratympanic fold present; dorsal color sandy brown to dark tan, often with four dark longitudinal stripes from head to pelvic region, plus partial dorsolateral stripe; throat, venter and parts of ventral thigh cream; throat may bear scattered darker markings; banding pattern on limbs; iris color sandy brown to amber, golden narrow edge around pupil; pupil horizontal; ear drum distinct.—This species avoids the forest and prefers open agricultural country or forest edges. It benefits from human activities and uses roadside ditches, flooded lawns, large puddles, or shallow agricultural ponds for reproduction. The species is commonly encountered and its calls heard around the Study Center area and its roads.

Polypedates macrotis (Boulenger, 1891): Dark-eared Tree Frog, Fig. 5i

Body slender with long hind limbs; head broad, rounded triangular in dorsal view; eyes big and noticeably directed forward; sharp canthus rostralis; toes and fingers expanded to broad blunt adhesive discs; not fully webbed toes; dorsal skin texture finely granular, without prominent tubercles; ventral skin of venter and thigh areolate; coloration light gray or ochre to tan above with dark spots or (sometimes) two dark stripes from snout to pelvis; area below supratympanic fold and most or all of tympanum masked in a dark brown marking that extends to flank; banding pattern on limbs; color of throat, venter and parts of ventral thigh is cream; throat and chest with some dark mottling; iris color brass to beige, with darker anterior and posterior sectors; pupil horizontal; ear drum distinct, large. —*Polypedates macrotis* often occurs in the same habitats with *P. otilophus*, such as forest clearing ponds or forest edge road ditches.

Polypedates otilophus (Boulenger, 1893): File-eared Tree Frog, Fig. 5j

Body slender to moderately robust (females); head edgy, broad, triangular; snout pointed; eyes big; saw-edged ridge above ear drum; hind limbs long, bearing distinct heel spur; fingers and toes expanded to large blunt adhesive discs; toes half webbed; color above grayish olive to yellowish light brown, fine longitudinal stripes on dorsum; thighs anteriorly and posteriorly banded with distinct zebra pattern; ventral side dirty white; ear drum visible, not embedded in dark marking; dorsal skin texture generally smooth (no prominent tubercles) but granulated above, distinctly areolate at flanks; venter skin areolate; iris beige, with fine black reticulations; pupil horizontal.—*Polypedates otilophus* is a species that uses clearings and forest edges for reproduction and, thus, can benefit from pond habitats created by human activities at forest edges, such as roadside ditches or village ponds. The species occurs in the vicinity of bodies of standing water at the Study Center. It is likely more widespread at Maliau Basin as the species is known to have a considerable elevational range in other regions of Borneo.

Rhacophorus borneensis Matsui, Shimada & Sudin, 2013: Borneo Flying Frog (acoustic identification; no photo)

No specimens were collected. Calls from the canopy, short in duration (approx. 1s) and composed of multiple

notes of moderately high pitch in fast sequence (resembling a woodpecker) were heard at the type locality and were interpreted as calls of this species as we have know these calls from other breeding populations of this species (the original species description does not provide a call description). No recordings were made. —*Rhacophorus borneensis* was formerly subsumed under the name *Rhacophorus reinwardtii* but has recently been established as a species of its own (Matsui et al. 2013b). Matsui et al. (2014) reported *R. borneensis* for the Nepenthes Camp area.

Rhacophorus cyanopunctatus Manthey & Steiof, 1998: Blue-spotted Tree Frog, Fig. 5k

Body slender with long hind limbs; large eyes; pointed snout, angular in lateral view; canthus rostralis sharply edged; toes and fingers expanded into adhesive discs; toes fully webbed except fourth toe; outer fingers webbed at base, inner fingers less; dorsal skin texture granulated; supratympanic fold present; dorsal color tan to mid brown with dark brown or green blotches; white spots or a white blotch below the eye; light blue spots at the otherwise black lower flank esp. towards groin and on anterior and posterior thigh as well as ventral shank; throat and venter white to cream; horizontal pupil; iris dark amber; ear drum visible, distinct.—*Rhacophorus cyanopunctatus* is a species associated with riparian-vegetation, breeding in small to medium sized streams of moderate velocity. Adults perch on overhanging vegetation above the streams. *R. cyanopunctatus* tadpoles are stream adapted and can cling to and venture into leaf litter at the side of the stream. Their mouth is a cup-shaped sucker (Leong 2004).

Rhacophorus pardalis Günther, 1858: Harlequin Flying Frog, Fig. 5l

Body slender (males) to robust (females); head broad and flat, large eyes; hand and foot large with extensive red webbing; toes and fingers terminally expanded; heal with small skin flap; dorsal skin texture finely granulated; color above brown with dark spots or faint dark marbling and occasional white spots; lower flanks and venter with distinctive marbling in yellow/black or yellow/red, respectively; iris yellowish beige peripherally and more brown towards center; pupil oval and horizontal; ear drum visible, indistinct in color.—Among the species of gliding frogs, *R. pardalis* is the most widely distributed and abundant species, and seems to be tolerant of moderate habitat alterations. It is most likely to be encountered at a variety of lentic aquatic habitats. The species was present around the Study Center and Nepenthes Camp. At the forest pond at Nepenthes Camp a sample of tadpoles was collected. Identification of tadpoles was based on size, body shape, coloration, tail fin shape, and oral disk features (Inger 1966, Malkmus et al. 2002, Haas et al. 2018)

Discussion

The present study contributes to the amphibian inventory of MBCA. Future research will certainly expand MBCA's species list further, if all elevations and habitat types are surveyed, what was not possible in our short survey. The accumulative species curve of the current assessment, did not indicate asymptotic saturation yet (Fig. 6) and more research will add to MBCA's inventory list. Progress in systematics will also refine the area's species list as difficult species complexes, such as the Creek Frog complex (McLeod 2010, Matsui et al. 2016), become resolved.

Considering the time invested and the experience of the searching participants in our survey the field campaign yielded results in the range that could be expected. For comparison, in 2009, a rapid assessment at Kubah National Park, Sarawak, with a slightly higher man-hrs investment (240 man-hrs) yielded 50 species (Haas, unpubl. data). Although different geographic and geological sites can only be compared with more elaborate study designs, this crude comparison suggests that the diversity encountered at MBCA in this campaign was only slightly less than expected for the amount of search effort invested.

During the period of our survey, we were struck by the low abundance of frogs and low reproductive activities. This may have been caused by a longer period of dry weather in the Maliau Basin before and during our survey. Low precipitation is not unusual for MBCA in the months of February and March (Tan et al. 2017) and other months may show higher reproductive activities in amphibians. In the light of the scarcity of published data (Ahmad and Wong 1998, Traeholt et al. 2007, Norhayati et al. 2010), it is premature to draw any conclusions about overall amphibian diversity at MBCA. Relatively low species diversity has been reported for other groups of organisms at Maliau Basin and has been attributed to Maliau's nutrient poor soils, acidic blackwater, and moderately productive vegetation, especially, its heath forests (Maryati et al. 1998, Hazebroek et al. 2004, Tan et. al 2017).

Four previous amphibian surveys conducted at MBCA had addressed amphibian diversity, i.e., Ahmad and Wong (1998), Lakim and Yambun (2002), Traeholt et al. (2007), and Norhayati et al. (2010). Matsui, Shimada, and Sudin worked on the amphibians of MBCA more recently and published descriptions of new species with Maliau Basin, Nepenthes Camp, as type locality (*Rhacophorus borneensis* in Matsui et al. 2013b, *Chiromantis inexpectatus* in Matsui et al. 2014). They mentioned some more species in their publications (see above), but did not publish a comprehensive species list of their expeditions. We compiled a list from the aforementioned sources and combined it with our own findings in Table 2.

Ahmad and Wong (1998) listed a total of 25 species of frogs among which three taxa could only be identified to the generic level (*Kalophrynus*, *Calluella* —now *Glyphoglossus*, see Frost 2018 for taxonomic details, and *Ansonia*). Frogs were collected by visual encounter trail

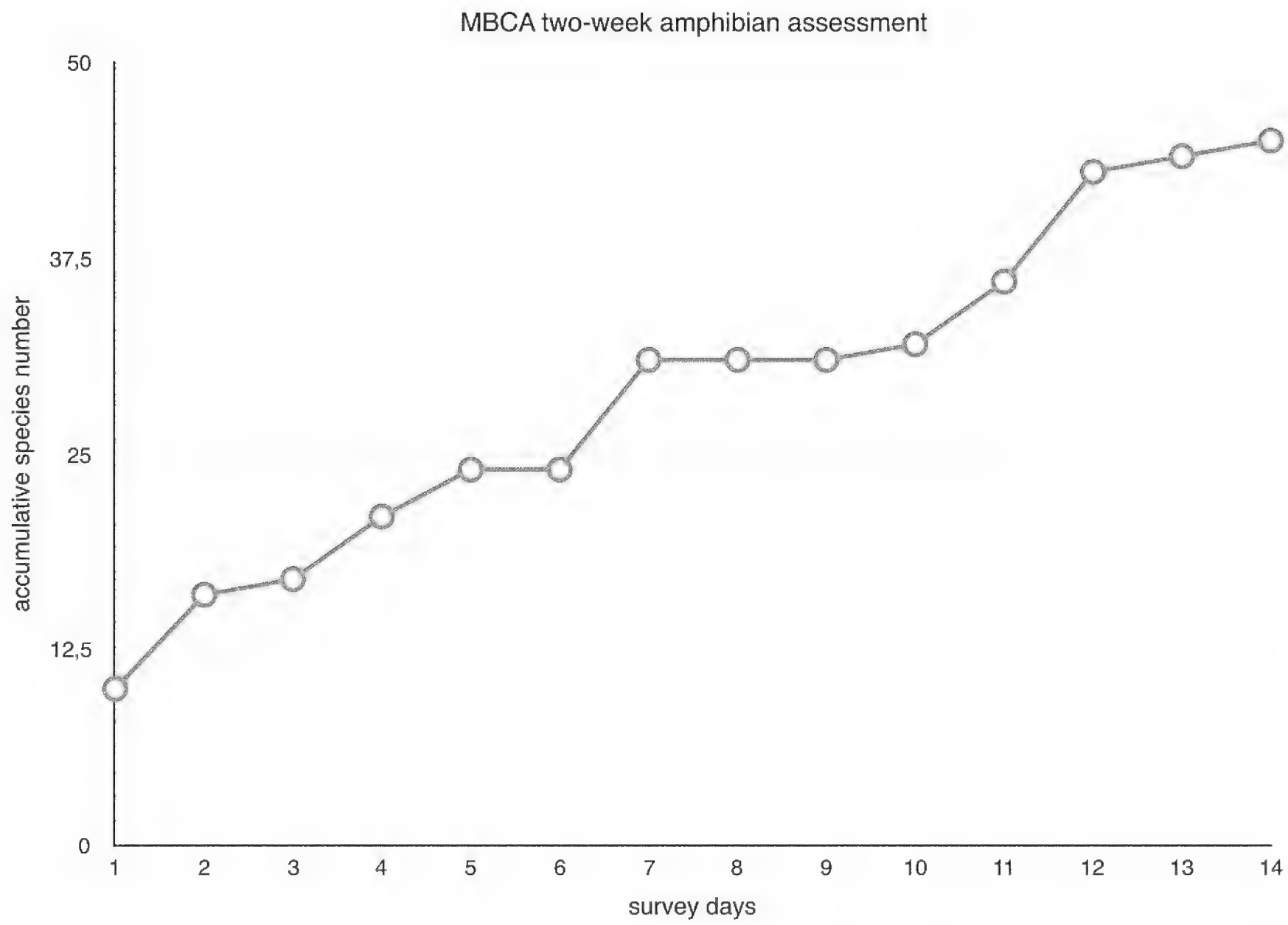

Figure 6. Accumulative species curve from species encounters at three sites within MBCA, 16 February 2017 to 2 March 2017.

walks at 11 different localities around their 1995 expedition camp; including only one named site, Dahl's Fall. Their localities fell in the submontane elevational zone and included heath forest (*Kerangas*) habitat. Species listed in their report and not encountered by our team include (Table 2): *Leptobrachium montanum*, *Rhacophorus gauni*, *Polypedates colletti*, *Glyphoglossus* sp., *Ansonia hanitschi*, and *Staurois tuberilinguis*. *Ansonia* has been subject to taxonomic changes since their paper (Matsui et al. 2007, 2010, Waser et al. 2016) and we think, according to current state of knowledge, it is highly likely that *A. hanitschi* in Ahmad and Wong (1998) is an unnamed taxon *Ansonia* sp. that corresponds to *Ansonia* sp. 3 in Matsui et al. (2010) by genetic evidence. Furthermore, we assume that *Kalophrynus* sp. in Ahmad and Wong (1998) represents *Kalophrynus* cf. *barioensis*, because this taxon was abundant in heath forest in their and our studies. Our specimen matched *K. barioensis* sequences at Genbank by 98%, despite presenting morphological differences to the original description of the species. Clearly more research is needed on this genus.

Interestingly, Ahmad and Wong (1998) mentioned that two *Kalophrynus* species were found together with eggs in a *Nepenthes* pitcher. The authors suggest that the species in question was a phytotelm breeder. Although we agree with this conclusion, we still want to point out that other species use pitchers for egg deposition as well (Das and Haas 2010) and the association of adults and eggs in one pitcher can be accidental; DNA analysis of eggs may be necessary to confirm the origin of such eggs (Hertwig et al. 2012).

Traeholt et al. (2007) visited nine sites, ranging from 305–991 m a.s.l.: Agathis Camp, Pakis Camp, Strike Ridge, Rafflesia Camp, Sawang Camp, Sungai Siput, Mudhill Creek, Pick-up road (Sawang Camp, Plot 2), Sungai Megapohn, thus, covering some sites that we did not sample. Traeholt's team worked 5–31 March 2001, similar in season and somewhat longer in period than our study. Their findings are summarized in Table 2. The team relied on visual encounters and pitfall traps. A total of 60 five-liter traps were installed during their study. Traeholt et al. (2007) reported two unidentified species, allocated to the genera *Rhacophorus* and *Philautus*. It was impossible to infer their identity but for the sake of overall species numbers, we assume that these taxa were covered by other studies (Tab. 2). Other species were mentioned by Traeholt et al. (2007) that we interpret differently on the background of current knowledge and recent progress in taxonomy. We take "*Rana chalconota*" in Traeholt et al. (2007) to represent *Chalcorana megalonesa* in our study. The latter taxon was separated from *C. chalconota* (Inger et al. 2009) and assigned to a new genus after the publication of Traeholt et al.'s (2007) report. Finally, also tentatively assume that *Leptolalax gracilis* is in fact *L. fritinniens* in our study according to current taxonomy; the latter has been delimited recently, is a common lowland species in Sabah, and is morphologically similar to *L. gracilis* (Dehling and Matsui 2013).

Lakim and Yambun (2002) investigated the amphibians of Lake Linumunsut. They reported a total of 26 species from that area. Notably two species, i.e., *Staurois latopalmatus* and *Rentapia hosii*, have only been reported in that survey for MBCA. Similar to our survey, Lakim and Yambun (2002) mentioned the scarcity of larval stages observed during their field work.

Norhayati et al. (2010) presented color photos for some of the species they encountered during their field campaign. They identified one species (*Metaphrynella sundana*) acoustically. For *Occidozyga sumatrana*, only the photo evidence exists, because the specimen escaped. A total of 11 species of amphibians were reported, two of which had not been reported for MBCA before (*Nyctixalus pictus*, *Philautus larutensis* then known as *P. petersi*).

Our work confirms many species that have already been known from previous studies (Table 2). Beyond the known species we expand MBCA's list of species by six: *Feihyla kajau*, *Hylarana erythraea*, *Limnonectes paramacrodon*, *L. ingeri*, *Kalophrynus meizon*, *Philautus nephophilus*. In addition, we report a total of four independent lineages of Creek Frogs that await description (Matsui et al. 2016), rather than the species "*Limnonectes kuhlii*" of previous studies. The new record for *Hylarana erythraea*, a human commensal in agricultural or logged areas, can be explained by the recent erection of the Maliau Study Center and its large pond. When compiling the updated species list, we proceeded in a conservative fashion and excluded some taxa with highly uncertain species identity (marked "sp." in the original publications) if no other species identity was highly plausible. We drew some conclusions about the identity of previously reported taxa (without available vouchers) based on taxonomic emendations that have happened in the meantime. Taking all taxonomic emendations and recent insights about phylogenetic relationships and proposed candidate species into account (esp. Matsui et al. 2010, Matsui et al. 2016), Table 2 lists a total of 61 taxa for MBCA, that includes four candidate Creek Frog species and one *Ansonia* sp. that was most likely what had been reported as *A. hanitschi* in earlier reports.

The species list is still preliminary, yet our account fills several gaps of its predecessors (Traeholt et al. 2007: tab. 3). The non-saturated curve of our sampling (Fig. 6) and the absence of certain other taxa from current records lets us predict that 61 does not represents the total amphibian species number for MBCA yet. Although we predict more species to be recorded for MBCA, this conservation area might harbour less amphibian species than Gunung Mulu (Das et al. 2017) or Gunung Kinabalu (Malkmus et al. 2002) because of its limited elevational range, less diverse substrate and vegetation types, and a relatively young geological age (Hazebroek et al. 2004). Endemic species and particularly mountain-top endemics have not yet been reported from MBCA. This may simply be due to inadequate sampling in highly inaccessible rim areas. Alternatively, mountain-top endemic species might not have had enough time to colonize from other mountains during favorable climatic times or to evolve *in situ* in the MBCA rim mountains. The only species that was thought for some time to be exclusive to Maliau Basin was *Chiromantis inexpectatus*; however, we now have unpublished evidence that this species occurs outside MBCA as well.

In groups of aquatic organisms, it has been argued that the typically black, humic acid rich, nutrient-poor water of the Maliau Basin streams (Tan et al. 2017) is the cause of reduced diversity of species (Hazebroek et al. 2004). Blackwater streams are known in tropical nutrient-poor white sand soils. In the case of MBCA, heath forest (*Kerangas*) is a typical nutrient-poor sand soil habitat. The humic acids stem from the secondary compound rich vegetation that grows on such poor soils and leaches out these compounds (Janzen 1974). Some frogs have been shown to be sensitive to low pH regimes and low pH may be toxic to their embryos (Saber and Dunson 1978). Larvae of other species, in contrast, seem to specialize on areas with high humic acid rich water such as peat swamps, for example *Ingerophrynus quadriporcatus*, *Polypedates colletti*, *Pulchrana baramica*, *Rhacophorus rufipes* (Haas and Das 2008, Haas et al. 2012); these species, however, have not been reported from Maliau yet. A notable number of Bornean frog species have evolved strategies to become independent of stream and pond water altogether. They are phytotelm breeders (*Kalophrynus*, *Metaphrynella*, *Nyctixalus*, *Rhacophorus harrissoni*) or species with direct development (some *Philautus*). Because of the biphasic complex life-cycle of amphibians and the various reproductive strategies that have evolved in frogs, the relation of species richness and blackwater may not be as straight forward as in other organisms. More research is needed to elucidate the relations of amphibian communities and habitat properties and MBCA may offer exceptional opportunities for such future work.

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References

Ahmad AH, Wong A (1998) The amphibian fauna of the Maliau Basin. In: Maryati M, Sinun W, Anton A, Dalimin MN, Ahmad AH (Eds) Maliau Basin Scientific Expedition, 12th–26th May 1996. Kota Kinabalu, 113–137.

Andersson LG (1923) Some reptiles and batrachians from Central Borneo. Meddelelser fra det Zoologiske Museum Oslo 7: 119–125.

Blyth E (1856 "1855") Report for October Meeting, 1855. Journal of the Asiatic Society of Bengal 24: 711–723.

Boulenger GA (1891) On new or little-known Indian and Malayan reptiles and batrachians. Annals and Magazine of Natural History, Series 6, 8: 288–292. https://doi.org/10.1080/00222939109460437

Boulenger GA (1893) Descriptions of new reptiles and batrachians obtained in Borneo by Mr. A. Everett and Mr. C. Hose. Proceedings of the Zoological Society of London 1893: 522–528.

Boulenger GA (1895) Descriptions of four new batrachians discovered by Mr. Charles Hose in Borneo. Annals and Magazine of Natural History, Series 6, 16: 169–173. https://doi.org/10.1080/00222939508680249

Boulenger GA (1918) Remarks on the batrachian genera *Cornufer*, Tschudi, *Platymantis*, Gthr., *Simomantis*, g. n., and *Staurois*, Cope. Annals and Magazine of Natural History, Series 9, 1: 372–375. https://doi.org/10.1080/00222931808562330

Boulenger GA (1920) A monograph of the South Asian, Papuan, Melanesian and Australian frogs of the genus *Rana*. Records of the Indian Museum 20: 1–226. https://doi.org/10.5962/bhl.title.12471

Chakrabarty P, Warren M, Page LM, Baldwin CC (2013) GenSeq: An updated nomenclature and ranking for genetic sequences from type and non-type sources. ZooKeys 346: 29–41. https://doi.org/10.3897/zookeys.346.5753

Chung AYC (2006) Biodiversity and Conservation of The Maliau Range. A Rain Forest in Sabah's Ultramafic Belt. Natural History Publications, Kota Kinabalu, 87 pp.

Cochran DM (1926) A new pelobatid batrachian from Borneo. Journal of the Washington Academy of Sciences 16: 446–447.

Das I, Jankowski A, Makmor MIB, Haas A (2007) Species diversity, elevational distribution and reproductive modes in an amphibian community at the Matang Range, Sarawak (Borneo). Mitteilungen des Hamburger Zoologischen Msueums und Instituts 104: 141–174.

Das I, Pui YM, Wahab T, Mokhtar S, Zainudin R (2017) A Checklist of the Amphibians and Reptiles of Gunung Mulu National Park, Sarawak. Ministry of Tourism, Culture, Youth and Sports, Kuching, 13 pp.

Das I, Haas A (2010) New species of *Microhyla* from Sarawak: Old World's smallest frogs crawl out of miniature pitcher plants on Borneo (Amphibia: Anura: Microhylidae). Zootaxa 2571: 37–52. http://www.mapress.com/j/zt/article/view/9403

Dehling M (2008) A new treefrog (Anura: Rhacophoridae: *Rhacophorus*) from Gunung Mulu, Borneo. Salamandra 44: 193–205. http://www.salamandra-journal.com/index.php/home/contents/2008-vol-44/70-dehling-j-m/file

Dehling JM, Dehling DM (2017) A new wide-headed fanged frog of the *Limnonectes kuhlii* group (Anura: Dicroglossidae) from western Borneo with a redescription of *Rana conspicillata* Günther, 1872. Zootaxa 4317: 291–19. https://doi.org/10.11646/zootaxa.4317.2.6

Dehling JM, Matsui M (2013) A new species of *Leptolalax* (Anura: Megophryidae) from Gunung Mulu National Park, Sarawak, East Malaysia (Borneo). Zootaxa 3670: 33–44. https://doi.org/10.11646/zootaxa.3670.1.2

Dehling JM, Matsui M, Imbun PY (2016) A new small montane species of *Philautus* (Amphibia: Anura: Rhacophoridae) from Gunung Kinabalu, Sabah, Malaysia (Borneo). Salamandra 52: 77–90. http://www.salamandra-journal.com/index.php/home/contents/2016-vol-52/565-dehling-j-m-m-matsui-p-yambun-imbun/file

Dring JCM (1983) Some new frogs from Sarawak. Amphibia-Reptilia 4: 103–115. https://doi.org/10.1163/156853883X00021

Frost DR (2018) Amphibian Species of the World: An Online Reference. Version 6.0 Electronic Database accessible at http://research.amnh.org/herpetology/amphibia/index.html. American Museum of Natural History, New York, USA. [accessed May 06, 2018]

Gravenhorst JLC (1829) Deliciae Musei Zoologici Vratislaviensis. Fasciculus primus. Chelonios et Batrachia. Leopold Voss, Leipzig. 104 pp.

Greer T (2002) Protected Area Management and Land Use Planning – Maliau Basin Conservation Area. Technical Assistance Report No. 36, Management of Maliau Basin Conservation Area Project. Kota Kinabalu, Yayasan Sabah-DANCED.

Guenette SA, Helie P, Beaudry F, Vachon P (2007) Eugenol for anaesthesia of African clawed frogs (*Xenopus laevis*). Veterinary Anaesthesia and Analgesia 34: 164–170. https://doi.org/10.1111/j.1467–2995.2006.00316.x

Günther ACLG (1858) Neue Batrachier in der Sammlung des britischen Museums. Archiv für Naturgeschichte. Berlin 24: 319–328. https://doi.org/10.5962/bhl.part.5288

Günther ACLG (1872) On the reptiles and amphibians of Borneo. Proceedings of the Zoological Society of London 1872: 586–600.

Goutte S, Ahmad Sah HH, Grafe TU (2017). Environmental correlates of species richness and composition of riparian anuran communities in rainforests of north-western Borneo: a metacommunity perspective. Herpetological Journal 27: 25-32. https://www.thebhs.org/publications/the-herpetological-journal/volume-27-number-1-january-2017

Goyes Vallejos J, Grafe TU, Ahmad Sah, HH, Wells K (2017) Calling behavior of males and females of a Bornean frog with male parental care and possible sex-role reversal Behavioral Ecology and Sociobiology 71: 95. https://doi.org/10.1007/s00265-017-2323-3

Haas A, Das I (2008) Larval identities of *Ansonia hanitschi* Inger, 1960 (Amphibia: Bufonidae) and *Polypedates colletti* (Boulenger, 1890) (Amphibia: Rhacophoridae) from East Malaysia (Borneo). Salamandra 44: 85–100. http://www.salamandra-journal.com/index.php/home/contents/2008-vol-44/56-haas-a-i-das/file

Haas A, Hertwig ST, Krings W, Braskamp E, Dehling JM, Min PY, Jankowski A, Schweizer M, Das I (2012) Description of three

Rhacophorus tadpoles (Lissamphibia: Anura: Rhacophoridae) from Sarawak, Malaysia (Borneo). Zootaxa 3328: 1–19. http://www.mapress.com/j/zt/article/view/13558

Haas A, Das I, Hertwig ST (2018) The Frogs of East Malaysia and their Larval Forms. http://www.frogsofborneo.org [accessed: May, 2018]

Hazebroek HP, Tengku ZA, Sinun W (2004) Maliau Basin. Sabah's lost world. Natural History Publications, Kota Kinabalu, 235 pp.

Hertwig ST, Lilje KE, Min PY, Haas A, Das I (2012) Molecular evidence for direct development in the rhacophorid frog, *Philautus acutus* (Rhacophoridae, Anura) from Borneo. The Raffles Bulletin of Zoology 60: 559–567. https://lkcnhm.nus.edu.sg/app/uploads/2017/06/60rbz559-567.pdf

Hertwig ST, Min PY, Haas A, Das I (2014) Dressed in black: A new *Ansonia* Stoliczka, 1870 (Lissamphibia: Anura: Bufonidae) from Gunung Murud, Sarawak, East Malaysia (Borneo). Zootaxa 3814: 419. https://doi.org/10.11646/zootaxa.3814.3.9

Imbun PY (2014) Amfibia Sabah. Dewan Bahasa dan Pustaka. Kuala Lumpur, 194 pp.

Inger RF (1960) A review of the Oriental toads of the genus *Ansonia* Stoliczka. Fieldiana. Zoology 39: 473–503. https://doi.org/10.5962/bhl.title.2697

Inger RF (1964) Two new species of frogs from Borneo. Fieldiana. Zoology 44: 151–159.

Inger RF (1966) The systematics and zoogeography of the Amphibia of Borneo. Fieldiana Zoology 66: 1–402.

Inger RF (2009) Contributions to the natural history of seven species of Bornean frogs. Fieldiana Zoology 116: 1–25. https://doi.org/10.3158/0015-0754-116.1.1

Inger RF, Frogner KJ (1979) New species of narrow-mouth frogs (genus *Microhyla*) from Borneo. Sarawak Museum Journal 27: 311–322.

Inger RF, Stuebing RB, Grafe U, Dehling M (2017). A Field Guide to the Frogs of Borneo (Second Edition). Third Edition. Natural History Publications, Kota Kinabalu, 228 pp.

Inger RF, Tan FL (1996) The Natural History of Amphibians and Reptiles in Sabah (2nd ed.). Natural History Publications, Kota Kinabalu, 101 pp.

Inger RF, Stuart BL, Iskandar D (2009). Systematics of a widespread Southeast Asian frog, *Rana chalconota* (Amphibia: Anura: Ranidae). Zoological Journal of the Linnean Society 155: 123–147. https://doi.org/10.1111/j.1096-3642.2008.00440.x

Janzen DH (1974) Tropical blackwater rivers, animals, and mast fruiting by the Dipterocarpaceae. Biotropica 6: 69–103. https://doi.org/10.2307/2989823

Kearse M, Moir R, Wilson A, Stones-Havas S, Cheung M, Sturrock S, Buxton S, Cooper A, Markowitz S, Duran C, Thierer T, Ashton B, Mentjies P, Drummond A (2012) Geneious Basic: an integrated and extendable desktop software platform for the organization and analysis of sequence data. Bioinformatics 28: 1647–1649. https://doi.org/10.1093/bioinformatics/bts199

Keller A, Rödel M-O, Linsenmair KE, Grafe TU (2009) The importance of environmental heterogeneity for species diversity and assemblage structure in Bornean stream frogs. Journal Animal Ecology 78, 305–314. https://doi.org/10.1111/j.1365-2656.2008.01457.x

Kiew BH (1978) The nomenclature and identity of the Javanese frog *Rana macrodon* Dumeril and Bibron. Malayan Nature Journal. Kuala Lumpur 31: 219–229.

Konopik O, Steffan-Dewenter I, Grafe TU (2015) Effects of logging and oil palm expansion on stream frog communities on Borneo, Southeast Asia. Biotropica 47: 636–643. https://doi.org/10.1111/btp.12248

Kueh BH (2004) Diversity of anurans at Trus Madi, Sabah. In: Maryati M, Matsui M, Kueh BH (Eds.) Herpetology and the Future Proceedings of the International Conference on Bornean Herpetology. University Malaysia Sabah, Kota Kinabalu, 26–29.

Kueh BH, Maryati M (2005) Anurans of protected areas in Sabah: Tabin Wildlife Reserve, Crocker Range Park and Maliau Basin Conservation Area. In: Tuen AA, Das I (Eds) Wallace in Sarawak–150 Years Later. Proceedings of an International Conference on Biogeography and Biodiversity. Universiti Malaysia Sarawak, Kota Samarahan, 182–187.

Kueh BH, Maryati M (2008) Anuran (frog and toad) explorations of Sabah, Borneo, for conservation, and public environmental awareness. In: Amphibian Workshop. Held 15–18 January 2008, Palace of the Golden Horses, MINES Resort City, Kuala Lumpur, 1–11.

Kueh BH, Maryati M, Das I, Chew D (2004) Integrated effort in the prioritization of areas for conservation in Borneo. Biodiversity Conservation Forward Together Proceedings of the BBEC International Conference. Universiti Malaysia Sarawak, Kota Kinabalu, 129–131.

Kueh BH, Norasmil I, Lau CES, Juelber A, Elangkumaran SS, Vyner-Bayang AN (2010a) *Rana luctuosa* (Mahogany Frog). Altitude and Maximum Size. Herpetological Review 41: 341–342. https://ssarherps.org/herpetological-review-pdfs/

Kueh BH, Tan LK, Voo TCH, Tan CT, Koh WS, Norasmil I, Juelber A (2010b) *Limnonectes kuhlii* (Kuhl's Creek Frog). Maximum Size. Herpetological Review 41: 338–339. https://ssarherps.org/herpetological-review-pdfs/

Lakim MB, Yambun P (2002) The herpetofauna and freshwater fishes of Linumunsut Lake, Maliau Basin, Sabah. Yayasan Sabah/DANCED, Kota Kinabalu, 13 pp.

Malkmus R, Manthey U, Vogel G, Hoffmann P, Kosuch J (2002) Amphibians & Reptiles of Mount Kinabalu (North Borneo). Koeltz Scientific Books, Koenigstein, 424 pp.

Manthey U, Grossmann W (1997) Amphibien & Reptilien Südostasiens. Natur und Tier Verlag, Münster, 512 pp.

Manthey U, Steiof U (1998) *Rhacophorus cyanopunctatus* sp. n. (Anura: Rhacophoridae), ein neuer Flugfrosch von der Malaiischen Halbinsel, Sumatra und Borneo. Sauria. Berlin 20: 37–42.

Maryati M, Sinun W, Anton A, Dalimin MN, Ahmad AH (1998) Maliau Basin Scientific Expedition 1996. Universiti Malaysia Sabah, Kota Kinabalu, 173 pp.

Matsui M (1979) Amphibians from Sabah I. Systematic and natural history notes. Contributions from the Biological Laboratory, Kyoto University 24: 303–346.

Matsui M (1986) Three new species of *Amolops* (Amphibia, Anura, Ranidae). Copeia 1986: 623–630.

Matsui M, Kuraishi N, Eto K, Hamidy A, Nishikawa K, Shimada T, Yambun P, Vairappan CS Hossman MYB (2016) Unusually high genetic diversity in the Bornean *Limnonectes kuhlii*-like fanged frogs (Anura: Dicroglossidae). Molecular Phylogenetics and Evolution 102: 305–319. https://doi.org/10.1016/j.ympev.2016.06.009

Matsui M, Mohamed M, Shimada T, Sudin A (2007a) Resurrection of *Staurois parvus* from *S. tuberilinguis* from Borneo (Amphibia, Ranidae). Zoological Science 24: 101–106. https://doi.org/10.2108/zsj.24.101

Matsui M, Nishikawa K, Yambun P (2013a) A new *Leptolalax* from the mountains of Sabah, Borneo (Amphibia, Anura, Megophryidae). Zootaxa 3753: 440–452. https://doi.org/10.11646/zootaxa.3753.5.3

Matsui M, Nishikawa K (2011) A new tiny *Kalophrynus* (Amphibia, Anura, Microhylidae) from northern Sarawak, Malaysian Borneo. Current Herpetology. Kyoto 30: 145–153. https://doi.org/10.5358/hsj.30.145

Matsui M, Shimada T, Liu W-Z, Maryati M, Khonsue W, Orlov N (2006) Phylogenetic relationships of Oriental torrent frogs in the genus *Amolops* and its allies (Amphibia, Anura, Ranidae). Molecular Phylogenetics and Evolution 38: 659–666. https://doi.org/10.1016/j.ympev.2005.11.019

Matsui M, Shimada T, Sudin A (2013b) A new gliding frog of the genus *Rhacophorus* from Borneo. Current Herpetology 32: 112–124. https://doi.org/10.5358/hsj.32.112

Matsui M, Shimada T, Sudin A (2014) First record of the tree-frog genus *Chiromantis* from Borneo with the description of a new species (Amphibia: Rhacophoridae). Zoological Science 31: 45–51. https://doi.org/10.2108/zsj.31.45

Matsui M, Tominaga A, Liu W, Khonsue W, Grismer LL, Diesmos AC, Das I, Sudin A, Yambun P, Yong H, Sukumaran J, Brown RM (2010) Phylogenetic relationships of *Ansonia* from Southeast Asia inferred from mitochondrial DNA sequences: Systematic and biogeographic implications (Anura: Bufonidae). Molecular Phylogenetics and Evolution 54: 561–570. https://doi.org/10.1016/j.ympev.2009.08.003

Matsui M, Yambun P, Sudin A (2007b) Taxonomic relationships of *Ansonia anotis* Inger, Tan, and Yambun, 2001 and *Pedostibes maculatus* (Mocquard, 1890), with a description of a new genus (Amphibia, Bufonidae). Zoological Science 24: 1159. https://doi.org/10.2108/zsj.24.1159

McLeod D (2010) Of Least Concern? Systematics of a cryptic species complex: *Limnonectes kuhlii* (Amphibia; Anura: Dicroglossidae). Molecular Phylogenetics and Evoltuion 56: 991–1000. https://doi.org/10.1016/j.ympev.2010.04.004

Mocquard F (1890) Recherches sur la faune herpetologique des iles de Bornéo et de Palawan. Nouvelles Archives du Muséum d'Histoire Naturelle, Série 3, Paris 2: 115–168.

Mocquard F (1892). Description de deux ophidiens et d'un batracien d'especes nouvelles. Le Naturaliste, Série 2. Paris 6: 35.

Norhayati A, Juliana S, Ahmad AH, Yousong H, Kasim J, Lojingi A, Kimmack A, Imbun P, Anuar MSS (2010) Herptefaunal records from the Eucalyptus Camp, Maliau Basin. In: Komoo I, Othman M, Said IM, Latiff A (Eds) Maliau Basin. Physical Environment and Biological Diversity of the Northern Rim. Kuala Lumpur, 246–254.

Oberhummer E, Barten C, Schweizer M, Das I, Haas A, Hertwig ST (2014) Description of the tadpoles of three rare species of megophryid frogs (Amphibia: Anura: Megophryidae) from Gunung Mulu, Sarawak, Malaysia. Zootaxa 3835: 59–79. https://doi.org/10.11646/zootaxa.3835.1.3

Pauly GB, Hillis DM, Cannatella DC (2004). The history of a Nearctic colonization: molecular phylogenetics and biogeography of the Nearctic toads (*Bufo*). Evolution 58: 2517–2535. https://doi.org/10.1554/04-208

Peters WCH (1867) Herpetologische Notizen. Monatsberichte der Königlichen Preussische Akademie der Wissenschaften zu Berlin 1867: 13–37.

Peters WCH (1871) Über neue Reptilien aus Ostafrica und Sarawak (Borneo), vorzüglich aus der Sammlung des Hrn. Marquis J. Doria zu Genua. Monatsberichte der Königlichen Preussische Akademie der Wissenschaften zu Berlin 1871: 566–581.

Pui YM, Das I (2016) Streams in forested headwaters as reservoirs of endemicity in Bornean amphibians. In: Das I, Tuen AA (Eds) Naturalists, explorers and field scientists in south-east Asia and Australasia. Topics in Biodiversity and Conservation, Volume 15. Springer International Publishing, Cham, Switzerland, 143–155. https://doi.org/10.1007/978-3-319-26161-4_9

Rödel M, Ernst R (2004) Measuring and monitoring amphibian diversity in tropical forests. I. An evaluation of methods with recommendations for standardization. Ecotropica 10: 1–14.

Saber PA, Dunson WA (1978) Toxicity of bog water to embryonic and larval anuran amphibians. Journal of Experimental Zoology Part B: Molecular and Developmental Evolution 204: 33–42. https://doi.org/10.1002/jez.1402040104

Schlegel H (1837) Abbildungen neuer oder unvollständig bekannter Amphibien, nach der Natur oder dem Leben entworfen, herausgegeben und mit einem erläuternden Texte begleitet. Part 1. Arnz & Co., Düsseldorf, 114 pp.

Schlegel H (1858) Handleiding tot de Beoefening der Dierkunde. Volume 2. Breda, Koninklijke Militaire Akademie, 628 pp.

Shimada T, Matsui M, Nishikawa K, Eto K (2015) A new species of *Meristogenys* (Anura: Ranidae) from Sarawak, Borneo. Zoological Science 32: 474–484. https://doi.org/10.2108/zs140289

Shimada T, Matsui M, Sudin A, Maryati M (2007) Identity of larval *Meristogenys* from a single stream in Sabah, Malaysia (Amphibia: Ranidae). Zoological Journal of the Linnean Society 151: 173–189. https://doi.org/10.1111/j.1096-3642.2007.00319.x

Shimada T, Matsui M, Yambun P, Lakim M, Mohamed M (2008) Detection of two cryptic taxa in *Meristogenys amoropalamus* (Amphibia, Ranidae) through nuclear and mitochondrial DNA analyses. Zootaxa 1843: 24–34. http://www.mapress.com/j/zt/issue/view/1938

Shimada T, Matsui M, Yambun P, Sudin A (2011a) A survey of morphological variation in adult *Meristogenys amoropalamus* (Amphibia, Anura, Ranidae), with a description of a new cryptic species. Zootaxa 2905: 1–24. http://www.mapress.com/j/zt/article/view/11249

Shimada T, Matsui M, Yambun P, Sudin A (2011b) A taxonomic study of Whitehead's torrent frog, Meristogenys whiteheadi, with descriptions of two new species (Amphibia: Ranidae). Zoological Journal of the Linnean Society 161: 157–183. https://doi.org/10.1111/j.1096-3642.2010.00641.x

Stoliczka F (1870) Observations on some Indian and Malayan Amphibia and Reptilia. Proceedings of the Asiatic Society of Bengal 1870: 103–109. https://doi.org/10.1080/00222937008696209

Tan SY, Sahana H, Kueh BH, Arman HF (2017) Evaluation of spatial and seasonal variations of dissolved organic matter in Maliau Basin, Sabah, Malaysia. Journal of Tropical Biology and Conservation 14: 105–124.

Tongkul F (2015) Waterfalls of Maliau Basin—Geoheritage of Sabah, Malaysian Borneo. Geoheritage 8: 1–11. https://doi.org/10.1007/s12371-015-0156-x.

Tongkul F, Chang FK (2003) Structural geology of the Neogene Maliau Basin, Sabah. Bulletin of the Geological Society Malaysia 47: 51–61.

Traeholt C (2001) Maliau Basin Conservation Project Zoological Survey. Management of Maliau Basin Conservation Area Project Technical Assistance Report No. 28. Yayasan Sabah-DANCED, 56 pp.

Traeholt C, Lundahl SLL, Pedeko D, Pilang V, Banggilon B, Dullah S, Bunggou MR, Sulaiman M (2007) Preliminary survey of amphibians in Maliau Basin Conservation Area, Sabah, Malaysia. Sabah Parks Nature Journal 8: 21–39.

Tschudi JJ von (1838) Classification der Batrachier mit Berücksichtigung der fossilen Thiere dieser Abtheilung der Reptilien. Neuchâtel: Petitpierre, 99 pp. https://doi.org/10.5962/bhl.title.4883

Müller S (1836) In: Van Oort P, Müller S Aantekkengingen gehouden op eene Reize over een Gedeelte van het Eiland Java, door de Le-

den der Natuurkundige Kommissie. Verhandelingen Bataviaasch Genootschap van Kunsten en Wetenschappen 16: 81–156.

Vences M, Thomas M, Bonett RM, Vieites DR (2005a) Deciphering amphibian diversity through DNA barcoding: chances and challenges. Philosophical Transactions of the Royal Society B: Biological Sciences 360: 1859–1868. https://doi.org/10.1098/rstb.2005.1717

Vences M, Thomas M, Van Der Meijden A, Chiari Y, Vieites DR (2005b) Comparative performance of the 16S rRNA gene in DNA barcoding of amphibians. Frontiers in Zoology 2: 5. https://doi.org/10.1186/1742-9994-2-5

Waser LE, Schweizer M, Haas A, Das I, Jankowski A, Min PY, Hertwig ST (2016) From a lost world: an integrative phylogenetic analysis of *Ansonia* Stoliczka, 1870 (Lissamphibia: Anura: Bufonidae), with the description of a new species. Organisms Diversity & Evolution 17: 1–19. https://doi.org/10.1007/s13127-016-0294-2

Webb CO, Ali S (2002) Plants and Vegetation of the Maliau Basin Conservation Area, Sabah, East Malaysia. Final Report to Maliau Basin Management Committee, 50 pp.

Yayasan Sabah (2014) Maliau Basin Conservation Area: Strategic Management Plan 2014–2023. Kota Kinabalu, Sabah: Yayasan Sabah Group, Kota Kinabalu, 245 pp. http://azkurs.org/pdfview/maliau-basin-conservation-area-sabah-malaysia-strategic-manage.html

Zug GR (2015) Morphology and systematics of *Kalophrynus interlineatus–pleurostigma* populations (Anura: Microhylidae: Kalphryninae) and a taxonomy of the genus *Kalophrynus* Tschudi, Asian Sticky Frogs. Proceedings of the California Academy of Sciences, 4th Series 62: 135–190.

Appendix 1

Specimen vouchers

Specimens examined from Maliau Basin Conservation Area. GenSeq nomenclature follows Chakrabarty (2013). NMBE=Naturhistorisches Museum Bern, Switzerland; HEP=BORNEENSIS Herpetological Collection at Institute for Tropical Biology and Conservation, Universiti Malaysia Sabah, Malaysia. SVL=Snout-Vent Length. ZMH=Zoologisches Museum Hamburg, Universität Hamburg, Germany. Sg.= Sungai (=River). Not all specimens were sequenced for mitochondrial genes. For those sequenced, GenBank accession numbers are included.

Bufonidae—*Ansonia spinulifer*, HEP 05916, SVL 34.0 mm, Ginseng Camp. *Ansonia spinulifer*, HEP 05917, SVL 33.0 mm, Ginseng Camp. *Ansonia spinulifer*, NMBE 1075464, SVL 37.7 mm, Ginseng Camp. *Ansonia spinulifer*, NMBE 1075465, SVL 42.7 mm, Ginseng Camp. *Ansonia spinulifer*, NMBE 1075466, SVL 34.7 mm, Ginseng Camp. *Ansonia spinulifer*, NMBE 1075467, SVL 34.3 mm, Ginseng Camp. *Ansonia longidigita*, HEP 05918, SVL 29.0 mm, Ginseng Camp. *Ansonia longidigita*, NMBE 1075463, SVL 53.2 mm, Ginseng Camp. *Ansonia leptopus*, NMBE 1075494, SVL 55.7 mm, Sg. Maliau side stream 3. *Ansonia* sp., NMBE 1075507, SVL 26.2 mm, Nepenthes Camp: Fawzy Fall. *Ansonia* sp., NMBE 1075508, SVL 26.4 mm, Nepenthes Camp: Fawzy Fall, accession MH537659 (genseq-4 16S). *Ansonia* sp., NMBE 1075509, SVL 24.5 mm, Nepenthes Camp: Fawzy Fall. *Ansonia* sp., NMBE 1075510, SVL 22.7 mm, Nepenthes Camp: Fawzy Fall. *Ansonia* sp., NMBE 1075511, SVL 26.4 mm, Nepenthes Camp: Fawzy Fall,. *Ansonia* sp., NMBE 1075512, SVL 27.3 mm, Nepenthes Camp: Fawzy Fall. *Ingerophrynus divergens*, HEP 05901, SVL 37.0 mm, Agathis Camp. *Ingerophrynus divergens*, NMBE 1075450, SVL 38.1 mm, Agathis camp. *Ingerophrynus divergens*, HEP 05905, SVL 37.0 mm, Wildlife Trail. *Ingerophrynus divergens*, NMBE 1075564, SVL 51.7 mm, Wildlife Trail. *Ingerophrynus divergens*, NMBE 1075465, SVL 33.2 mm, Wildlife Trail. *Ingerophrynus divergens*, NMBE 1075479, SVL 36.6 mm, left side Sg. Maliau. *Ingerophrynus divergens*, NMBE 1075480, SVL 38.5 mm, left side Sg. Maliau. *Leptophryne borbonica*, NMBE 1075469, SVL 22.3 mm, Ginseng Camp. *Phrynoidis juxtasper*, HEP 05886, Study Center. *Phrynoidis juxtasper*, HEP 05894, Belian Trail. *Phrynoidis juxtasper*, HEP 05895, Belian Trail. *Phrynoidis juxtasper*, NMBE 1075487, SVL 44.4 mm, Sg. Maliau: side stream 1. *Phrynoidis juxtasper*, NMBE 1075515, SVL 110.0 mm, Nepenthes Camp: Fawzy Fall. *Phrynoidis juxtasper*, tadpole sample, ZMH A12578–9, ZMH A12647: GenBank MG909569 (genseq-4, 16S, tVal), Sg. Maliau.

Dicroglossidae—*Fejervarya limnocharis*, HEP 05888, Study Center. *Fejervarya limnocharis*, NMBE 1075557, SVL 41.8 mm, Study Center. *Limnonectes ingeri*, NMBE 1075454, SVL 32.6 mm, Belian Trail, accession MH537636 (genseq-4 16S). *Limnonectes ingeri*, NMBE 1075455, SVL 102.04 mm, Belian Trail, accession MH537637 (genseq-4 16S). *Limnonectes ingeri*, HEP 05891, SVL 38.0 mm, Belian Trail, accession MH537638 (genseq-4 16S). *Limnonectes leporinus*, HEP 05893, 52.0 mm, Sg. Maliau side stream 2, accession MH537639 (genseq-4 16S). *Limnonectes leporinus*, HEP 05897, SVL 115.0 mm, Sg. Maliau side stream 1. *Limnonectes leporinus*, HEP 05900, SVL 50.0 mm, Agathis Camp, accession MH537645 (genseq-4 16S). *Limnonectes leporinus*, HEP 05902, SVL 56.0 mm, Agathis Camp, accession MH537646 (genseq-4 16S). *Limnonectes leporinus*, HEP 05911, SVL 63.0 mm, Ginseng Camp. *Limnonectes leporinus*, NMBE 1075485, SVL 93.3 mm, Sg. Maliau: side stream 1. *Limnonectes paramacrodon*, NMBE 1075490, SVL 43.9 mm, Sg. Maliau: side stream 2, accession MH537641 (genseq-4 16S). *Limnonectes paramacrodon*, NMBE 1075559, SVL 59.8 mm, Study Center. *Limnonectes paramacrodon*, NMBE 1075570, SVL 55.4 mm, Wildlife Trail. *Limnonectes paramacrodon*, HEP 05887, 68.0 mm, Study Center, accession MH537635 (genseq-4 16S). *Limnonectes paramacrodon*, HEP 05904, Wildlife Trail. *Limnonectes* sp., HEP 05908, SVL 32.0 mm, Sg. Maliau side stream 3, accession MH537651 (genseq-4 16S). *Limnonectes* sp., HEP 05919, SVL 18.0 mm, Ginseng

Camp. *Limnonectes* sp., NMBE 1075451, SVL 28.4 mm, Agathis camp, accession MH537647 (genseq-4 16S). *Limnonectes* sp., NMBE 1075470, SVL 64.5 mm, Ginseng Camp, accession MH537656 (genseq-4 16S). *Limnonectes* sp., NMBE 1075471, SVL 34.9 mm, Ginseng Camp. *Limnonectes* spec., NMBE 1075481, SVL 22.6 mm, left side Sg. Maliau, accession MH537648 (genseq-4 16S). *Limnonectes* sp., NMBE 1075482, SVL 26.2 mm, left side Sg. Maliau, accession MH537649 (genseq-4 16S). *Limnonectes* sp., NMBE 1075491, SVL 35.4 mm, Sg. Maliau side stream 2, accession MH537643 (genseq-4 16S). *Limnonectes* sp., NMBE 1075499, SVL 43.5 mm, Sg. Maliau side stream 3, accession MH537652 (genseq-4 16S). *Limnonectes* sp., NMBE 1075500, SVL 35.3 mm, Sg. Maliau side stream 3, accession MH537653 (genseq-4 16S). *Limnonectes* spec., NMBE 1075514, SVL 35.5 mm, Nepenthes Camp: Fawzy Fall.

Megophryidae—*Leptobrachium abbotti*, HEP 05923, SVL 67.0 mm, Nepenthes Camp, Waterfall Trail. *Leptobrachium abbotti*, HEP 05926, SVL 50.0 mm, Nepenthes Camp, Stream 1. *Leptobrachium abbotti*, NMBE 1075521, SVL 52.6 mm, Nepenthes Camp: Nepenthes Garden. *Leptobrachium abbotti*, NMBE 1075554, SVL 68.6 mm, Nepenthes Camp: Waterfall Trail. *Leptobrachium abbotti*, NMBE 1075567, SVL 23.6 mm, Wildlife Trail. *Leptobrachium abbotti*, NMBE 1075568, SVL 69.4 mm, Wildlife Trail. *Leptobrachium abbotti*, NMBE 1075569, SVL 40.9 mm, Wildlife Trail. *Leptolalax* spec., NMBE 1075495, SVL 30.6 mm, Sg. Maliau side stream 3. *Leptolalax*,spec., NMBE 1075496, SVL 32.5 mm, Sg. Maliau side stream 3. *Leptolalax* spec., NMBE 1075497, SVL 30.8 mm, Sg. Maliau side stream 3. *Leptolalax* spec., NMBE 1075498, SVL 30.1 mm, Sg. Maliau side stream 3. *Megophrys nasuta*, NMBE 1075456, SVL 58.8 mm, Belian Trail.

Microhylidae—*Microhyla berdmorei*, HEP 05896, Belian Trail. *Microhyla berdmorei*, HEP 05903, Wildlife Trail. *Microhyla berdmorei*, NMBE 1075492, SVL 23.4 mm, Sg. Maliau side stream 2. *Microhyla berdmorei*, NMBE 1075493, SVL 33.3 mm, Sg. Maliau side stream 2. *Microhyla berdmorei*, NMBE 1075561, SVL 32.7 mm, Study Center: road to Belian Camp. *Microhyla petrigena*, NMBE 1075545, SVL 12.8 mm, Nepenthes Camp: pond. *Microhyla petrigena*, NMBE 1075546, SVL 16.7 mm, Nepenthes Camp: pond. *Kalophrynus* cf. *barioensis*, NMBE 1075505, SVL 18.7 mm, Nepenthes Camp: Agathis trail, accession MH537660 (genseq-4 16S). *Kalophrynus* cf. *barioensis*, NMBE 1075506, SVL 18.6 mm, Nepenthes Camp: Agathis trail, accession MH537661 (genseq-4 16S).

Ranidae—*Amnirana nicobariensis*, HEP 05890, Study Center. *Chalcorana megalonesa*, NMBE 1075448, SVL 30.8 mm, Agathis camp, accession MH537644 (genseq-4 16S). *Chalcorana megalonesa*, NMBE 1075468, SVL 49.4 mm, Ginseng Camp. *Chalcorana megalonesa*, NMBE 1075483, SVL 45.7 mm, Sg. Maliau side stream 1. *Chalcorana megalonesa*, NMBE 1075489, SVL 34.7 mm, Sg. Maliau side stream 2, accession MH537642 (geneq-4 16S). *Chalcorana megalonesa*, NMBE 1075556, SVL 33.3 mm, Sg. Maliau side stream 1. *Chalcorana raniceps*, HEP 05915, Ginseng Camp. *Huia cavitympanum*, NMBE 1075513, SVL 68.9 mm, Nepenthes Camp: Fawzy Fall. *Hylarana erythraea*, HEP 05884, SVL 30.0 mm, Study Center. *Hylarana erythraea*, HEP 05885, SVL 33.0 mm, Study Center. *Hylarana erythraea*, HEP 05889, 33.0 mm, Study Center. *Hylarana erythraea*, NMBE 1075558, SVL 56.5 mm, Study Center. *Hylarana luctuosa*, NMBE 1075527, SVL 52.2 mm, Nepenthes Camp: pond. *Hylarana picturata*, HEP 05892, 35.0 mm, Belian Trail. *Hylarana picturata*, HEP 05909, SVL 37.0 mm, Sg. Maliau side stream 4. *Hylarana picturata*, NMBE 1075449, SVL 50.2 mm, Agathis camp. *Hylarana picturata*, NMBE 1075484, SVL 37.00 mm, Sg. Maliau side stream 1. *Hylarana picturata*, NMBE 1075563, SVL 36.8 mm, Wildlife Trail. *Hylarana signata*, NMBE 1075544, SVL 43.2 mm, Nepenthes Camp: pond. *Meristogenys orphnocnemis*, HEP 05907, SVL 40.0 mm, Sg. Maliau side stream 3, accession MH537650 (genseq-4 16S). *Meristogenys orphnocnemis*, HEP 05912, SVL 40.0 mm, Ginseng Camp, accession MH537655 (genseq-4 16S). *Meristogenys orphnocnemis*, HEP 05914, SVL 40.0 mm, Ginseng Camp. *Meristogenys orphnocnemis*, NMBE 1075472, SVL 36.5 mm, Ginseng Camp. *Meristogenys orphnocnemis*, NMBE 1075473, SVL 65.5 mm, Ginseng Camp, accession MH537657 (genseq-4 16S). *Meristogenys orphnocnemis*, NMBE 1075474, SVL 34.3 mm, Ginseng Camp. *Meristogenys orphnocnemis*, NMBE 1075475, SVL 65.6 mm, Ginseng Camp. *Meristogenys orphnocnemis*, NMBE 1075476, SVL 67.0 mm, Ginseng Camp, accession MH537658 (genseq-4 16S). *Meristogenys orphnocnemis*, NMBE 1075486, SVL 40.2 mm, Sg. Maliau side stream 1, accession MH537640 (genseq-4 16S). *Meristogenys orphnocnemis*, NMBE 1075501, SVL 40.3 mm, Sg. Maliau side stream 3, accession MH537654 (genseq-4 16S). *Meristogenys orphnocnemis*, NMBE 1075502, SVL 35.7 mm, Sg. Maliau side stream 3. *Meristogenys orphnocnemis*, NMBE 1075503, SVL 69.8 mm, Sg. Maliau side stream 3. *Odorrana hosii*, NMBE 1075477, SVL 85.5 mm, Ginseng Camp. *Staurois guttatus*, HEP 05899, SVL 34.0 mm, Agathis Camp. *Staurois guttatus*, HEP 05910, SVL 53.0 mm, Sg. Maliau side stream 5. *Staurois guttatus*, HEP 05913, SVL 51.0 mm, Ginseng Camp. *Staurois guttatus*, NMBE 1075452, SVL 50.1 mm, Agathis camp. *Staurois guttatus*, NMBE 1075453, SVL 31.4 mm, Agathis camp. *Staurois guttatus*, NMBE 1075488, SVL 53.2 mm, Sg. Maliau side stream 1. *Staurois tuberilinguis*, HEP 05929, Nepenthes Camp, Fawzy Fall. *Staurois tuberilinguis*, HEP 05930, Nepenthes Camp, Fawzy Fall. *Staurois tuberilinguis*, HEP 05931, Nepenthes Camp, Fawzy Fall. *Staurois tuberilinguis*, HEP 05932, Nepenthes Camp, Fawzy Fall. *Staurois tuberilinguis*, NMBE 1075516,

SVL 28.5 mm, Nepenthes Camp: Fawzy Fall. *Staurois tuberilinguis*, NMBE 1075517, SVL 29.0 mm, Nepenthes Camp: Fawzy Fall. *Staurois tuberilinguis*, NMBE 1075518, SVL 34.4 mm, Nepenthes Camp: Fawzy Fall. *Staurois tuberilinguis*, NMBE 1075519, SVL 30.3 mm, Nepenthes Camp: Fawzy Fall. *Staurois* spec., NMBE 1075520, SVL 28.4 mm, Nepenthes Camp: Fawzy Fall. *Staurois tuberilinguis*, NMBE 1075555, SVL 29.6 mm, Nepenthes Camp: Fawzy Fall.

Rhacophoridae—*Chiromantis inexpectatus*, HEP 05922, SVL 25.0 mm, Nepenthes Camp Pond. *Chiromantis inexpectatus*, NMBE 1075525, SVL 23.8 mm, Nepenthes Camp: pond. *Chiromantis inexpectatus*, NMBE 1075526, SVL 25.8 mm, Nepenthes Camp: pond. *Chiromantis inexpectatus* tadpole, ZMH A12597, GenBank accession: MG909568 (genseq-4, 16S, tVal), Nepenthes Camp: pond. *Feihyla kajau*, HEP 05925, SVL 20.0 mm, Nepenthes Camp, Waterfall Trail. *Feihyla kajau*, NMBE 1075551, SVL 20.7 mm, Nepenthes Camp: Waterfall Trail. *Feihyla kajau*, NMBE 1075552, SVL 20.0 mm, Nepenthes Camp: Waterfall Trail. *Kurixalus appendiculatus*, HEP 05906, SVL 35.0 mm, Wildlife Trail. *Kurixalus appendiculatus*, NMBE 1075553, SVL 49.5 mm, Nepenthes Camp: Waterfall Trail. *Kurixalus appendiculatus*, NMBE 1075566, SVL 34.0 mm, Wildlife Trail. *Philautus hosii*, NMBE 1075478, SVL 40.8 mm, Ginseng Camp. *Philautus nephophilus*, NMBE 1075522, SVL 20.1 mm, Nepenthes Camp: Nepenthes Garden, accession MH537662 (genseq-4 16S). *Philautus nephophilus*, NMBE 1075523, SVL 17.5 mm, Nepenthes Camp: Nepenthes Garden, accession MH537663 (genseq-4 16S). *Philautus nephophilus*, NMBE 1075524, SVL 18.0 mm, Nepenthes Camp: Nepenthes Garden. *Polypedates leucomystax*, NMBE 1075560, SVL 42.1 mm, Study Center. *Polypedates macrotis*, NMBE 1075462, SVL 75.5 mm, Belian Trail. *Polypedates macrotis*, NMBE 1065571, SVL 55.5 mm, Wildlife Trail. *Polypedates otilophus*, NMBE 1075562, SVL 73.2 mm, Study Center. road to Belian Camp. *Rhacophorus cyanopunctatus*, HEP 05927, SVL 31.0 mm, Nepenthes Camp, Stream 1. *Rhacophorus cyanopunctatus*, HEP 05928, SVL 30.0 mm, Nepenthes Camp, Stream 1. *Rhacophorus cyanopunctatus*, NMBE 1075548, SVL 31.2 mm, Nepenthes Camp: stream 1. *Rhacophorus cyanopunctatus*, NMBE 1075549, SVL 29.2 mm, Nepenthes Camp: stream 1. *Rhacophorus cyanopunctatus*, NMBE 1075550, SVL 31.7 mm, Nepenthes Camp: stream 1. *Rhacophorus pardalis*, HEP 05924, SVL 46.0 mm, Nepenthes Camp, Stream 1. *Rhacophorus pardalis*, NMBE 1075504, SVL 44.9 mm, Nepenthes Camp: stream 1. *Rhacophorus pardalis*, NMBE 1075547, SVL 56.6 mm, Nepenthes Camp: pond. *Rhacophorus pardalis*, NMBE 1075572, SVL 46.5 mm, Wildlife Trail.